

## ORIGINAL PAPER

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**Shoot dynamics of the giant grass *Gynerium sagittatum* in Peruvian Amazon floodplains, a clonal plant that does show self-thinning**

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**Abstract** The giant rhizomatous grass *Gynerium sagittatum* is an early successional species that forms dense monocultures in Peruvian Amazon floodplains. We studied the shoot population structures by recording shoot densities and shoot heights. Leaf areas and stem volumes were allometrically estimated. Stands of two varieties of *G. sagittatum* were examined that differ in height and in the degree of shoot branching. In stands of increasing age, marked decreases in shoot densities were accompanied with an increase in mean shoot size. Self-thinning was indicated by the negative correlation between log stem volume per unit ground area and log shoot density, significant at least for one of the two varieties. The difference in thinning slope between the varieties could be largely accounted for by their different shoot geometry, as was revealed by calculations based on the allometric model of Weller (1987b). The relationship between log leaf area per shoot and log shoot density was significantly negative with slopes close to  $-1$ . Shoot size inequalities decreased with increasing mean stem volume per shoot, probably as a result of density-dependent mortality of the smaller shoots. All of these results accord with expectations for shoot self-thinning. *Gynerium sagittatum* is the first clear example of a clonal plant species that exhibits

self-thinning in natural monospecific stands. It is argued that self-thinning occurs in this giant tropical grass because its shoots are perennial and do not experience seasonal die-back (periodic density-independent mortality), in contrast to many of the clonal plant species that have been studied so far.

**Key words** Clonal plants · Self-thinning · Allometry  
Shoot dynamics · Amazon floodplains

**Introduction**

The self-thinning dynamics of plant monocultures are characterized by an increase in mean plant biomass associated with a decrease in plant density, as a result of density-dependent mortality (e.g. White 1980; Westoby 1984; Weller 1987a; Lonsdale 1990; Silvertown and Lovett Doust 1993). As an outstanding exception, shoot populations of clonal plants appear not to self-thin. Hutchings (1979) showed that developing natural stands of a variety of clonal plants do not progress along a self-thinning trajectory, but stop accumulating biomass as the thinning line is reached. The anomaly is widely accepted, as indicated by the decision of Lonsdale (1990) to exclude *Populus tremuloides* from the data set that he used to recalculate the self-thinning statistics because the species “grows clonally and therefore would not necessarily be expected to comply with the thinning rule”.

Despite considerable research we still know very little why clonal plants do not exhibit self-thinning. Originally, the deviant behaviour was related to the observation that shoots of clonal plants are often interconnected (Hutchings 1979; Pitelka 1984; Hutchings and Bradbury 1986). It was suggested that they respond to increasing density in a coordinated way, resulting in a prevention of shoot overproduction and in clonal support of small shaded shoots. However, reviewing the

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data on shoot competition in clonal plants, de Kroon (1993) recently concluded that the evidence for this hypothesis is scant. For example, the widely observed negatively density-dependent shoot natality (e.g. Briske and Butler 1989; Hartnett 1993) can be more readily explained by a reduction of meristem activity induced by the local light climate in dense stands, than by integration (de Kroon and Kwant 1991). Although there is evidence that early shoot growth is supported in clonal plants (Bradbury 1981; Hutchings 1983; Hara et al. 1993), the high mortality of the smaller shoots in dense stands (Hutchings and Barkham 1976; Bradbury 1981; van der Toorn and Mook 1982; Cain 1990; de Kroon et al. 1992; Hara et al. 1993) also challenges the notion that integration has a prominent effect on shoot dynamics.

Negative density-dependent shoot natality alone cannot explain the lack of self-thinning. Westoby (1984) argued that shoots of clonal plants have a "maximum size" that limits the trajectory over which self-thinning can occur. Once stands reach the self-thinning line, shoots have already accumulated a major part of their maximum biomass. Little additional growth of the extant shoots and therefore little density-dependent shoot mortality will occur before growth stops. Westoby's hypothesis is appealing because it may explain the general lack of shoot self-thinning in stands of clonal plants, irrespective of the genotypic composition of the population and the degree of shoot interconnectedness. The "maximum shoot size" seems to be related to the seasonality of growth of the shoots of many clonal plant species. When stand biomass peaks in summer, shoots stop growing, resources are directed towards belowground storage organs, and flowering and end-of-season shoot senescence begin.

The hypothesis of Westoby (1984) has received surprisingly little attention so far. In order to test the hypothesis we studied the shoot dynamics of the grass *Gynerium sagittatum* in dense natural monospecific stands in the Peruvian Amazon. *G. sagittatum* is very suitable for such a test. Its shoots may reach heights up to 10–15 m after several years of growth in the continuous growing season of the tropics (Kalliola et al. 1992). Except for its giant size and the longevity of its shoots, *G. sagittatum* resembles temperate clonal plant species in many respects. For example, seedling recruitment is absent or occurs only during the establishment phase of stands and shoots are interconnected by perennial rhizomes (Kalliola et al. 1992). In fact, *Gynerium* is taxonomically closely related to common reed (*Phragmites*) (Renvoize 1980) for which shoot self-thinning could not be demonstrated (Hutchings 1979; Mook and van der Toorn 1982).

In stands of *G. sagittatum* of increasing age, densities of live and dead shoots were recorded, and shoot sizes were evaluated in terms of height, leaf area and stem volume (as a substitute for biomass). For self-

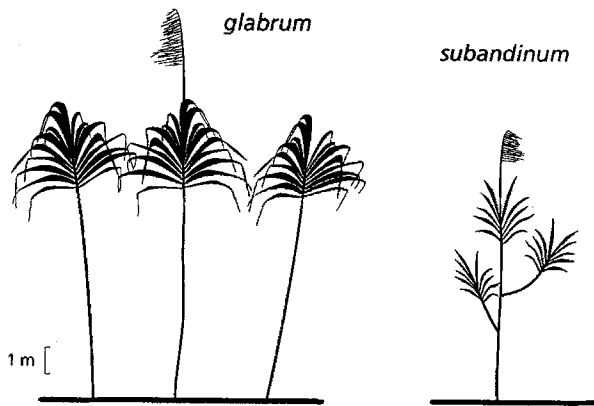
thinning stands the following results are expected. The correlation between log stem volume per unit ground area and log shoot density should be significantly negative (Weller 1987a; Lonsdale 1990). Because evidence is accumulating that self-thinning dynamics are closely related to shoot geometry (Lonsdale and Watkinson 1983a; Weller 1987b; Ellison 1987, 1989; Verwijst 1989; Osawa and Allen 1993), the actual value of the thinning slope should match the value predicted on the basis of allometric growth parameters. In addition, slopes based on the correlation between log mean leaf area per shoot and log shoot density were computed, with expected values of  $-1$  (under constant leaf area index, LAI) or slightly steeper (when LAI increases during self-thinning), irrespective of the steepness of the self-thinning slope (Mohler et al. 1978; Hutchings and Budd 1981; Norberg 1988). Finally, because self-thinning is the result of asymmetric competition and density-dependent shoot mortality (e.g. Mohler et al. 1978; Weiner and Thomas 1986), the increase in mean shoot size during self-thinning is expected to be accompanied by a decrease in shoot size inequality (Weiner and Whigham 1988; Knox et al. 1989; Thomas and Weiner 1989; Yokozawa and Hara 1992).

## Materials and methods

### The species

*Gynerium sagittatum* (Aubl.) P. Beauv. ("caña brava") is a rhizomatous reed-grass with stout shoots (culms) and long leaf blades which are clustered towards the top of the shoot, forming a fan-shaped summit (Fig. 1). The species is widely distributed throughout tropical South America and is characteristic for river floodplains, swamps and other early successional habitats (Kalliola et al. 1992; Kalliola and Renvoize, 1994). In our study area in Amazonian Peru, *G. sagittatum* is a common early colonizer of sandy river banks (Kalliola et al. 1991). The species forms dense monocultures until trees invade that overtop and outcompete *G. sagittatum*. Successional zones can readily be identified from young stands near the river margin to old stands near the tree line (Kalliola et al. 1992; Lamotte 1992). The sites are annually flooded during the wet season resulting in the deposition of fresh sandy sediment in *G. sagittatum* vegetation. Occasionally, outer zones of stands are washed away during heavy flooding which may result in a discontinuous zonation.

In Peru, two distinct varieties of *G. sagittatum* are known that differ in a number of morphological and reproductive characteristics (Fig. 1; Kalliola et al. 1992; Kalliola and Renvoize, 1994). Variety *glabrum* forms almost unbranched shoots that may reach a height of 8–15 m, containing more than 25 leaves each about 200 cm long and 10 cm wide. This variety depends exclusively on vegetative reproduction; seedlings of this type are extremely rare. River banks adjacent to *glabrum* stands are colonized by rhizomes and stolons that grow out from established plants, as well as by regeneration from fragmented rhizomes and shoots that are washed ashore. Var. *glabrum* forms extensive, 50–200 m wide stands at practically every meander loop along the small and medium-sized rivers in southern Peru. Shoots of the variety *subandinum* remain smaller (up to 5–8 m height) and may branch profusely (Fig. 1). Each branch may have about 20 leaves with a length of 130 cm and



**Fig. 1** *Gynierium sagittatum* shoot morphology. Variety *glabrum* is taller and mostly unbranched while variety *subandinum* stays smaller but may branch profusely. In addition both varieties differ in a number of other morphological characters such as leaf shape and hairiness (Kalliola and Renvoize, 1994)

a width of up to 5 cm. New sites are usually colonized by abundant seedling establishment and in young stands the shoots of a seedling occur in clumps. Established seedlings expand by rhizome and stolon formation. Var. *subandinum* is characteristic of the larger rivers in northern Peru where it may occupy areas up to 1–2 km<sup>2</sup> at the meander loops or on channel islands. This *G. sagittatum* variety may dominate in zones of several hundreds of metres wide until trees become dominant.

## Methods

In June–July 1992, five meanders with dense undisturbed *G. sagittatum* vegetation were studied, three with *glabrum* monocultures along the river Madre de Dios in southern Peru (12° 30' S, 70° 30' W) and two with *subandinum* along the river Ucayali in northern Peru (5° 00' S, 74° 00' W). Quadrats along a transect were classified in the following developmental stages which all represent almost pure *G. sagittatum* stands, devoid of canopy trees: “Edge” (E), the youngest stand with a closed canopy at the well-illuminated margin adjacent to the sandy beach; “Young” (Y) in which most of the medium-sized shoots still bear leaf blades from near the shoot base; an “Intermediate” phase (I) with taller shoots and leaves clustered towards the top of the shoot and in which vines and herbs appear in the understorey; “Adult” (A) with more abundant flowering and growth of understorey herbs, and lianas that occasionally reached the top of the canopy; “Old” (O), the oldest *G. sagittatum* monostands still devoid of canopy trees. Not all stages were present in all meanders probably due to erosion of parts of the population in the past. Edge plots are lacking for *subandinum*; the youngest stands closest to the river were typically composed of seedlings with clumped shoots forming a relatively open canopy and were discarded in this study. Our sampling did not include “senescing” stages (Kalliola et al. 1992) where successional trees overgrow *G. sagittatum* resulting in their decline.

In principle one quadrat per meander and per developmental stage was analysed, ranging in size from 8 m<sup>2</sup> (stage E) to 50 m<sup>2</sup> (stage O). All living, dead, flowering and juvenile shoots were counted and harvested. Even the smallest shoots were easy to find. Dead shoots had lost all green leaf tissue. Juvenile shoots were shoots that had not yet formed expanded leaves. Most, if not all juvenile shoots were of vegetative origin. For all living and dead shoots the number of lateral branches was counted. The lengths of the main stem and each of the branches (up to the base of the highest leaf) and, for lateral branches, the height of the point of attachment to the main stem were measured to the nearest dm. For many dead shoots these records were incomplete because branches were

broken or partly decayed. In addition, the following measurements were taken for all living shoots: the diameter of the main stem at soil level (to the nearest mm), the phenological status of each of the branches (living, dead, flowering), and for all living branches, the number of green leaves, and the lengths and largest widths of two leaves of average age and size (at opposite sides of the summit). A total of 1605 living and 2446 dead shoots were measured.

The leaf area was estimated allometrically as follows. For twenty leaves of various length, the leaf width at every 10-cm interval from base to leaf tip was measured, in addition to the leaf length and largest width (separately for *glabrum* and *subandinum*). Each of the leaves were cut from paper (to scale) in the laboratory, and the area was measured with a LiCor 3100 leaf area meter. The allometric relationships of individual leaf area ( $A$ ) on length ( $L$ ) and largest width ( $W$ ) were  $A = 0.625 \times L \times W$  ( $r^2 = 0.998$ ) for *glabrum* and  $A = 0.677 \times L \times W$  ( $r^2 = 0.991$ ) for *subandinum*. The leaf area per branch was obtained by multiplying mean leaf area per leaf with the number of leaves per branch.

Stem volume of trees is a widely used and excellent predictor of tree biomass (e.g. Knox et al. 1989). For *G. sagittatum*, the stem volume of the main stem ( $V$ ) was calculated as  $V = L \times \pi \times (\frac{1}{2}D)^2$  with  $L$  as the stem length and  $D$  as the stem diameter. The volume of the thinner lateral branches was calculated in a similar way using half of the diameter of the main stem. Total shoot stem volume was the sum of the volumes of all living branches. If a dead main stem had living branches, the volume of the main stem was included in the shoot stem volume up to the point of attachment of the highest living branch.

## Data analysis

Shoot self-thinning was verified by the following four steps.

1. Prior to an analysis of thinning lines, suspect data points should be eliminated (e.g. Weller 1987a; Lonsdale 1990). For stands that undergo self-thinning, stem volume per unit ground area should increase with time (e.g. Weller 1987a; Silvertown and Lovett Doust 1993) and the leaf area index (LAI) should be constant or increase as well (Mohler et al. 1978; Hutchings and Budd 1981; Norberg 1988). An inspection of these trends seems particularly relevant in our study in which self-thinning is investigated in natural stands of an early successional species. At some point in succession *G. sagittatum* is replaced by other species and the population will decline. Such decline which will first appear as reductions in stem volume and LAI.

2. Following recommendations in Weller (1987a), we calculated slope  $\beta_0$  of the relationship between log stem volume per unit ground area and log shoot density with Principal Component Analysis (PCA) (Sokal and Rohlf 1981, p. 596). A significant negative slope is an indication of self-thinning. The correlation between log mean leaf area per shoot and log shoot density was analysed in a similar way.

3. Weller's (1987b) allometric model gives equations to calculate the self-thinning slope on the basis of the changes in shoot allometry. The average height – average mass allometric exponent  $\theta$  was calculated by a PCA of log mean height on log mean stem volume, and the transformed thinning exponent  $\phi$  was calculated as  $\phi = 0.5 - 0.5\theta$  (assuming that  $\delta = 0$ , i.e. that the biomass per unit of canopy volume remains unchanged during self-thinning). The allometrically derived thinning slope  $\beta_1$  is then calculated as  $\beta_1 = \gamma + 1$  with  $\gamma = -1/(2\phi)$  (see Weller 1987b; Verwijst 1989 and Osawa and Allen 1993 for details). Slopes  $\beta_1$  for *glabrum* and *subandinum* are compared with the actual self-thinning slopes  $\beta_0$ .

4. In order to investigate the expectation that shoot size inequalities decrease during self-thinning, the unbiased Gini coefficients (Weiner and Solbrig 1984; Knox et al. 1989) were calculated based on shoot stem volume. The Gini coefficient lies between 0, for a population consisting of individuals that are all of equal size, and 1, for a population in which all individuals except one are infinitesimally small. Differences in Gini coefficient were tested for

significance by comparing bootstrapped confidence intervals, based on 250 bootstrap repetitions. Because these intervals are generally too narrow (Dixon et al. 1987), the 99% rather than 95% confidence intervals were used for this purpose.

## Results

### Shoot densities and shoot sizes

Live shoot densities dropped approximately seven- (*glabrum*) and three-fold (*subandinum*) from the youngest to the oldest stands (Fig. 2). The decline was most pronounced at the younger stages. In all stands large numbers of dead shoots were counted, often exceeding the number of living shoots (results not shown). Dead shoot densities were particularly high at the Young and Intermediate stages of *subandinum* populations (10–40 m<sup>-2</sup>). Flowering in *glabrum* was erratic. Up to about 10% of all living shoots flowered except in the youngest stands (stage E) in which no flowering occurred. It was always the main stem that flowered and at the time of our study all flowering stems had died (but they often had one or more living lateral branches). In *subandinum* the flowering percentage increased as stands matured, culminating at 20–30% in the oldest stands. In this variety shoots frequently had several flowering as well as vegetative branches and nearly all flowering branches were alive. The number of juvenile shoots was small for both varieties (approximately 0.5 m<sup>-2</sup> or less), except in the younger *subandinum* stands (2–11 m<sup>-2</sup>), and tended to decline as stands matured. With increasing stand age, an increasing proportion of the juveniles was dead, up to about 40% (*glabrum*) and 80% (*subandinum*) in the oldest stands.

The decline in shoot density as stands matured was accompanied with an increase in mean shoot size. The size increment ranged was four- to five-fold (*glabrum*) and two- to three-fold (*subandinum*) in terms of shoot height (Fig. 3), and was even more marked in terms of shoot stem volume or shoot leaf area (results not shown). On average, *glabrum* shoots contained fewer than 1.5 living branches (including the live main stem), while the number of dead branches per shoot peaked at a mean of 1 per shoot in the Adult stage (Fig. 4). The oldest stands (stage O), however, were almost exclusively composed of very tall unbranched shoots. Branching was more luxuriant in *subandinum* and increased with stand age to a mean of 3 living and 2–3 dead lateral branches per shoot in the oldest stands (Fig. 4).

In the younger stands (stages Edge, Young and Intermediate), intact dead shoots were small with a mean height of only 20–50% of the mean height of living shoots. However, dead shoot height will be underestimated because up to about 30% of the dead shoots

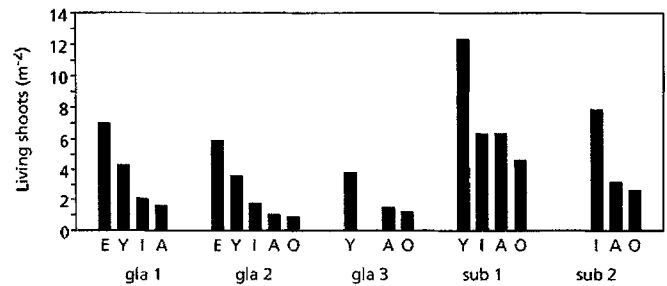


Fig. 2 Densities of living shoots in quadrats of *G. sagittatum* of increasing age, for three populations of var. *glabrum* (gla1-3) and two of var. *subandinum* (sub1-2). Stand age classes are “Edge” (E), “Young” (Y), “Intermediate” (I), “Adult” (A), and “Old” (O)

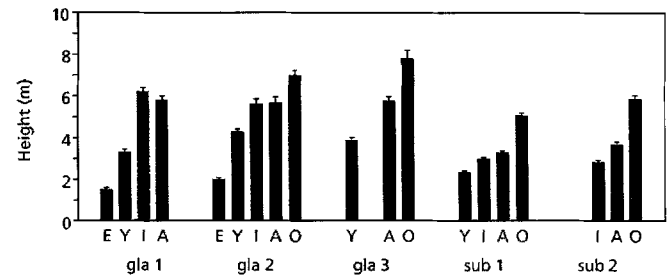


Fig. 3 Mean shoot height ( $\pm$  SE) in quadrats of *G. sagittatum* of increasing age, for three populations of var. *glabrum* (gla1-3) and two of var. *subandinum* (sub1-2). Stand age classes as in Fig. 2

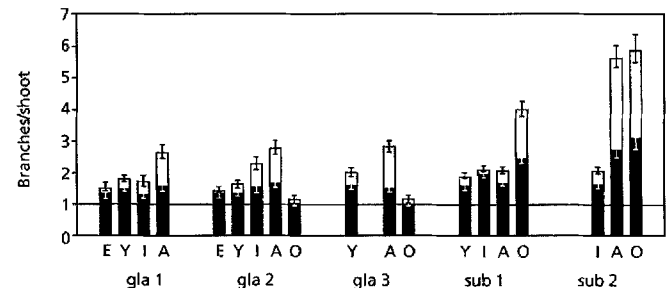
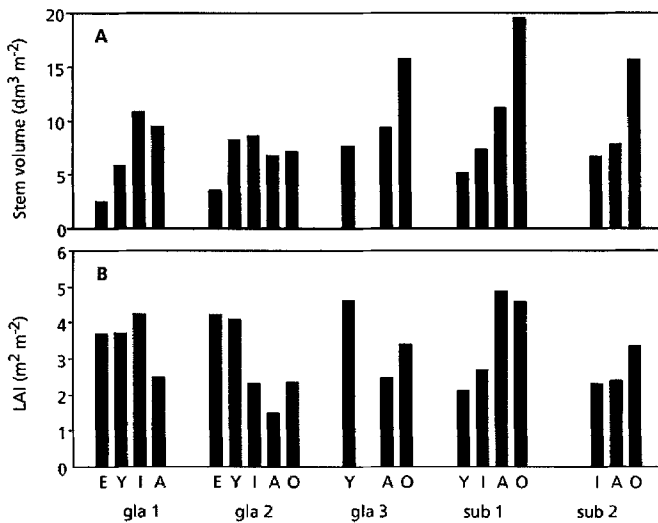


Fig. 4 Mean number of living (solid bars) and dead branches (open bars) per living shoot ( $\pm$  SE), including the main stem, in quadrats of *G. sagittatum* of increasing age, for three populations of var. *glabrum* (gla1-3) and two of var. *subandinum* (sub1-2). The solid line at 1 branch/shoot indicates that living shoots have, by definition, at least one living branch. Stand age classes as in Fig. 2

were broken in stands of these stages, and larger dead shoots had a higher change of breakage. In older stands the proportion of broken shoots increased dramatically and no size estimates for the dead shoots could be obtained.

### An analysis of shoot self-thinning

In populations subjected to self-thinning, declining shoot densities as seen in Fig. 2 should be accompanied by an increase in stem volume per unit ground area and a constant or increasing LAI. For *glabrum*, only the relatively early stand development conformed to these prerequisites (Fig. 5); in older stands stem

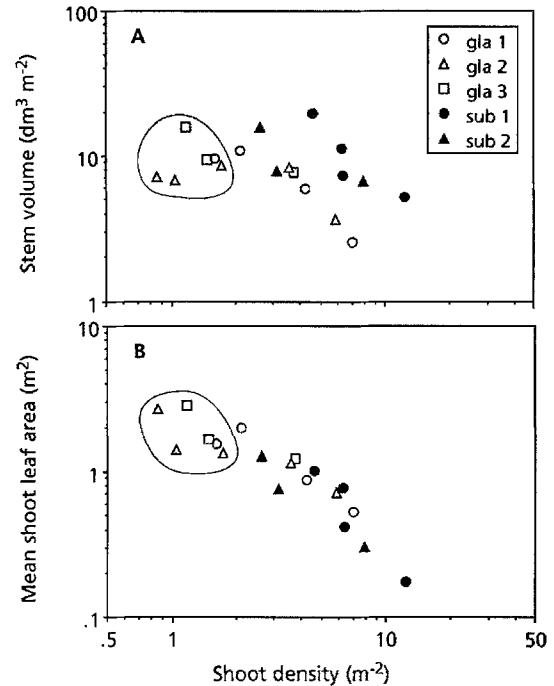


**Fig. 5** **A** Total stem volume per unit ground area, and **B** total leaf area per unit ground area (LAI), for three populations of var. *glabrum* (*gla1-3*) and two of var. *subandinum* (*sub1-2*). Stand age classes as in Fig. 2

volume no longer increased and/or LAI declined. Therefore, self-thinning statistics were analysed for a subset of six *glabrum* stands with approximately similar and high LAI (3.5–4.5). In *subandinum* populations stem volume and LAI continued to increase up to the oldest stands and self-thinning may be expected to occur along the entire stand age gradient.

The self-thinning graph for stem volume is given in Fig. 6A. For *glabrum* the first principal component (slope  $\beta_e = -1.335$ ) was highly significant but this was not the case for *subandinum* ( $P > 0.05$ ). However, slope  $\beta_e$  of *subandinum* ( $-0.853$ ) was steeper than the “ideal” slope of  $-0.5$  (Westoby 1984; Weller 1987a) and very close to statistical significance (lower 95% confidence limit was  $-0.007$ ). The lack of significance seems to be caused in part by the small sample size ( $n = 7$ ). The PCA slope of log leaf area on log shoot density was slightly higher for *subandinum* ( $-1.378$ ) than for *glabrum* ( $-1.110$ ) (Fig. 6B); neither was significantly different from  $-1$ .

The steeper self-thinning slope of *glabrum* compared to *subandinum* accords with a priori expectations on



**Fig. 6** **A** The relationship between log total stem volume per unit ground area and log shoot density. The principal component analysis (PCA) slopes  $\beta_e$  are  $-1.335$  ( $r^2 = 0.91$ ) and  $-0.853$  ( $r^2 = 0.44$ ) for *glabrum* and *subandinum*, respectively. **B** The relationship between log mean shoot leaf area and log shoot density, with slopes  $-1.110$  ( $r^2 = 0.97$ ) and  $-1.378$  ( $r^2 = 0.80$ ) for *glabrum* and *subandinum*, respectively [open symbols var. *glabrum* (combined data for three populations, *gla1-3*), solid symbols var. *subandinum* (combined data for two populations, *sub1-2*)]. The encircled *glabrum* stands were excluded from the analysis (see text)

the basis of the differences in shoot geometry (e.g. Miyaniishi et al. 1979; Ellison 1987; Weller 1987b; Verwijst 1989). The former variety grows taller (Fig. 3) than the latter with less radial expansion (less branching, Fig. 4; see also Fig. 1). Consequently, a given amount of biomass can be added with less attendant mortality in *glabrum* than in *subandinum* and this implies a steeper thinning slope. Calculations based on Weller’s (1987b) allometric model substantiate this expectation quantitatively. For both varieties, the empirical slopes  $\beta_e$  fall within the 95% confidence interval of the allometrically derived slopes  $\beta_a$  (Table 1).

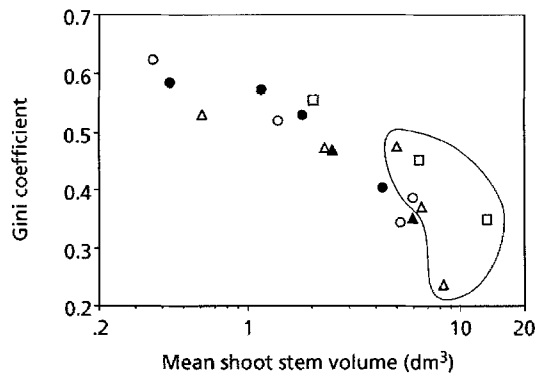
**Table 1** The empirical thinning slope  $\beta_e$  as calculated from the relationship between stand stem volume and shoot density (Fig. 6A), the average height – average mass allometric exponent  $\theta$ , the transformed thinning exponent  $\phi$  and the allometrically derived thinning

	$\beta_e$	$\theta$	$\phi^a$	$\beta_a^b$
Var. <i>glabrum</i>	$-1.335$	0.538	0.231	$-1.167$
95% C.I.	$(-2.17; -0.88)$	$(0.50; 0.58)$	$(0.25; 0.21)$	$(-0.98; -1.40)$
Var. <i>subandinum</i>	$-0.853$	0.356	0.322	$-0.553$
95% C.I.	$(-5.99; -0.01)$	$(0.25; 0.47)$	$(0.38; 0.26)$	$(-0.33; -0.90)$

<sup>a</sup> $\phi = 0.5 - 0.5\theta$

<sup>b</sup> $\beta_a = \gamma + 1$ , with  $\gamma = -1/(2\phi)$

slope  $\beta_a$ , for two *Gynerium sagittatum* varieties that differ in shoot geometry. The values of  $\beta_e$  and  $\theta$ , as well as their 95% confidence intervals (C.I.), were calculated by principal component analysis (PCA). Based on Weller’s (1987b) allometric model



**Fig. 7** The relationship between the Gini coefficient and log mean shoot size, both based on mean shoot stem volume, for var. *glabrum* (open symbols) and var. *subandinum* (solid symbols). The PCA slopes are  $-0.197$  ( $r^2=0.74$ ) and  $-0.216$  ( $r^2=0.87$ ) for *glabrum* and *subandinum*, respectively. The encircled *glabrum* stands were excluded from the analysis (see text). Symbols as in Fig. 6

Hence, the difference between the thinning slopes of the *G. sagittatum* varieties can be largely explained by their different geometry.

A decline in shoot size inequality was expected during self-thinning as a result of density-dependent mortality of the smaller shoots. In accordance with this expectation, the correlation between Gini coefficient and mean shoot size was significantly negative for both varieties (Fig. 7). In four out of five *G. sagittatum* populations, the Gini coefficient of shoot stem volume indeed decreased significantly ( $P < 0.01$ ) with increasing stand age. This decrease was insignificant in the remaining population, probably because the Gini coefficient of the youngest stand was lacking as a result of missing data.

## Discussion

### Self-thinning in *G. sagittatum*

There is substantial evidence that shoot self-thinning occurs in natural monocultures of the rhizomatous grass *G. sagittatum*. Four types of evidence have been provided:

1. Stand development through time is characterized by decreasing shoot densities (Fig. 2), increasing stand biomass (here evaluated as stem volume; Fig. 5A), and constant or increasing LAI (Fig. 5B). These trends are necessary conditions for self-thinning (Weller 1987a; Hutchings and Budd 1981; Silvertown and Lovett Doust 1993). They distinguish the *G. sagittatum* stand development from the "competition-density" effect and the trajectory described by the "law of constant final yield" (e.g. Westoby 1984; Silvertown and Lovett Doust 1993).

2. Self-thinning is demonstrated by the negative correlations between log stem volume and log shoot

density (significant at least for var. *glabrum*; Fig. 6A). The significant negative relationships between log shoot leaf area and log shoot density with slopes slightly steeper than  $-1$  (Fig. 6B) also accord with expectations for self-thinning.

3. The actual thinning slopes of the two varieties *glabrum* and *subandinum* are similar to the slopes predicted on the basis of their shoot geometry (Table 1). Note, as Weller (1987b) points out, that such agreement will occur only if data are collected from stands that actually undergo self-thinning. Allometric models have recently been very successful in explaining self-thinning relationships (Weller 1987b; Verwijst 1989; Osawa and Allen 1993; see also Ellison 1987, 1989; Hara et al. 1991; Weiner and Thomas 1992).

4. Density-dependent shoot mortality and self-thinning are a result of asymmetric competition (e.g. Mohler et al. 1978; Westoby 1984; Weiner and Thomas 1986). The decreasing size inequality with increasing mean shoot size (Fig. 7) accords with observations for self-thinning stands of annuals and trees (Weiner and Thomas 1986; Weiner and Whigham 1988; Thomas and Weiner 1989; Knox et al. 1989). These relationships are remarkably similar for the two varieties, in spite of their different thinning lines, and their slopes (about  $-0.20$ ) are similar to values reported in the literature. It should be noted, however, that the causes of shoot mortality are unclear from our study. Some of the high mortality amongst the smallest shoots in the younger *G. sagittatum* stands may have its origin in periodic flooding, rather than in above-ground competition for light.

Beyond the self-thinning phase, the older *glabrum* stands showed signs of decline such as a decreasing LAI (Fig. 5). At the oldest stage only the very tall, almost unbranched shoots survive (Figs. 3, 4). The reasons for this decline are unknown, and it is also unclear why it is not shown by *subandinum*. It was not caused by tree shading because there were no canopy trees present in any of the quadrats that we studied. The declining density of stands of *glabrum* may be important for succession. The growth of early successional tree species like *Cecropia membranacea* that invade *G. sagittatum* vegetation (Kalliola et al. 1992; Lamotte 1992) will be enhanced and this may accelerate the development towards tropical rain forest. The self-thinning *subandinum* stands may be much more persistent and inhibit succession for a longer time than those of the giant *glabrum* variety.

### Implications for shoot self-thinning in stands of clonal plants

*G. sagittatum* is the first unambiguous example of a clonal plant that experiences asymmetric shoot competition and self-thinning in monospecific stands. As emphasized above, this giant tropical grass resembles temperate clonal herbs (especially dominant

graminoids such as *Phragmites*, *Typha*, and *Carex* species) in many respects. However, for none of these temperate species could shoot self-thinning be demonstrated (Hutchings 1979; Mook and van der Toorn 1982; Lonsdale and Watkinson 1983b; Dickerman and Wetzel 1985; Lapham and Drennan 1987). Hence, our results corroborate the contention of Westoby (1984) that the occurrence of self-thinning is constrained by the maximum size that shoots of clonal plants can achieve. If shoots can markedly increase in size after the thinning line is reached, as in the case of *G. sagittatum*, the shoot dynamics are not different from non-clonal plants.

As Westoby (1984) noted, all plants have some maximum size that places an upper limit to the trajectory along which self-thinning may occur. The pertinent question is therefore why nearly all shoot populations of clonal plants exhibit little self-thinning before this maximum size is reached, in contrast to non-clonal plants like annuals and trees. Two factors seem important in this respect. First, vegetative shoot recruitment is negatively density-dependent in nearly all clonal plant species that have been studied (see de Kroon and Kwant 1991; de Kroon 1993, and references therein). As a result, crowded stands reach the thinning line at relatively low densities when shoots have accumulated already a significant part of their maximum size. By contrast, annual plants with a similar maximum size seem less effective in preventing overcrowding and may reach thinning lines at considerably higher densities.

Second, the actual sizes that shoots of many clonal species reach is determined by the seasonality of growth and mortality. Many clonal plant species that grow in dense monospecific stands have annual shoots, and, even if shoots are perennial, most of the above-ground biomass senesces at the end of the growing season. This periodic density-independent mortality curtails the period in which size hierarchies can develop, that would eventually result in density-dependent mortality and self-thinning. Furthermore, a synchronisation of the growth among shoots, as they emerge each spring from basal meristems, may retard the formation of shoot hierarchies (de Kroon 1993). Both factors, periodic density-independent mortality and density-dependent shoot natality in spring, will amplify each other in preventing self-thinning in clonal plants.

The significance of the seasonal die-back of the above-ground biomass for the apparent lack of self-thinning in many clonal species is confirmed by observations on populations of clonal trees. Stands of species like *Castanea sativa* (Ford and Newbould 1970) and *Populus tremuloides* (Weller 1987a, based on forestry data from Baker 1925) have been shown to self-thin. There is also tentative evidence that shoot populations of dwarf bamboo (*Sasa* spp.), rhizomatous species with perennial shoots up to about 1.5 m in height, exhibit self-thinning (Makita 1992 and unpublished work;

Makita et al. 1993). For each of these species, as well as for *G. sagittatum* in our study, stands form a perennial structure and shoot size hierarchies develop over several years of growth. We conclude that the seasonality of stand development is one of the major factors that may explain why self-thinning is absent in many clonal plant species. To date the significance of this factor has been widely overlooked.

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