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Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama

ELAINE HOOPER,[1,2,3,4] RICHARD CONDIT,[2] AND PIERRE LEGENDRE[3]

[1]Department of Biology, McGill University, 1205 Dr. Penfield Ave, Montreal, Quebec, Canada H3A 1B1

[2]Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948 USA

[3]Départment de Sciences Biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

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[4] Corresponding address: Laboratoire de Pierre Legendre, Department de Sciences Biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

Abstract. Deforestation in the tropics often leads to unproductive agriculture, and results in abandoned, degraded grasslands that tree species re-colonize poorly. To evaluate why forests do not regenerate naturally, and to identify potential species for use in reforestation of degraded areas, we planted 15,000 seeds of twenty native tree species varying in seed size and shade-tolerance, in abandoned Panamanian farmland dominated by the exotic grass, *Saccharum spontaneum*. To determine the effects of above- and below-ground constraints on tree seedling germination, survival, and growth, we utilized four mowing and shading treatments of the *Saccharum*. Shading the *Saccharum* effectively eliminated it, whereas mowing led to increased light above-ground, but did not reduce *Saccharum* growth rate. Germination, survival, and growth of tree seedlings approximately doubled in shade treatments, compared to the unshaded control, but were lowest when the *Saccharum* was mown three times. Fire significantly decreased germination and survival.

Some species did not follow these general trends, though, and we identified four species groups that varied in their response to *Saccharum* competition. Very small-seeded, light demanding species performed poorly, and we do not recommend their use in reforestation because they tolerate neither above- nor below-ground constraints imposed by the *Saccharum*. Light-demanding species with large seeds were limited by above-ground constraints, namely shading. Small-seeded, shade-tolerant species were limited by below-ground constraints imposed by the *Saccharum*. Large-seeded, moderately to highly shade-tolerant species performed well in the *Saccharum;* we recommend a reforestation strategy which includes planting this last group.

Keywords: abandoned farmland; natural regeneration; Panama; *Saccharum spontaneum*; secondary succession; tropical reforestation.

INTRODUCTION

Deforestation has left vast areas of primary humid tropical forest in a degraded state (Houghton *et al.* 1991). Central America, for example, is now 10% abandoned agricultural land (Finegan 1992). Land rehabilitation through re-establishment of native trees is becoming increasingly attractive, since native trees have been shown to improve soil conditions significantly within four years on badly degraded tropical land (Fisher 1995). Facilitating natural tree regeneration may be an important management option, but significant barriers to tree regeneration must be overcome. Lack of seed dispersal is often cited as a major limitation to natural regeneration (Guevara *et al*. 1986, Janzen 1988, Nepstad *et al*. 1990, Vieira *et al*. 1994, Aide and Cavelier 1994, Aide *et al*. 1995, da Silva *et al*. 1996), and harsh microsite characteristics including low nutrient status, high irradiance, high temperature, and low soil moisture during the dry season can also limit tree seedling survival (Uhl *et al.* 1988, Nepstad 1989, Nepstad *et al*. 1990, Gerhardt 1993).

These physiological stresses are worsened when abandoned lands are invaded by exotic grasses that compete with tree seedlings for moisture and nutrients (Nepstad 1989) and increase the propensity for fire (D'Antonio and Vitousek 1992). In Panama, abandoned sites in the Canal area are invaded by the exotic, invasive grass, *Saccharum spontaneum* L. ssp. *spontaneum*. *Saccharum* attains an average height of 2.5 m and grows in dense, impenetrable stands. It is drought-adapted, burns frequently, and does not yield to weeding, mulching, fire, or deep plowing because of its deep rhizomes (Panje 1970). It is listed as one of the most serious weeds in Indonesia, India, Thailand, the Philippines, and Puerto Rico (Holm *et al.* 1979).

Reforestation options in *Saccharum* grasslands have not been studied, but there has been considerable research on tree restoration of deforested tropical sites invaded by a similar grass species (*Imperata cylindrica)* in South-East Asia. Nevertheless, no feasible large-scale method has been found for restoring the original tree cover. Planting indigenous tree seedlings directly into the *Imperata* had limited success because of the physical difficulty of planting, grass competition, allelopathy, fire susceptibility, as well as soil degradation and compaction (Kuusipalo *et al.* 1995). Intensive deep plowing followed by planting of a fast-growing exotic tree crop to suppress grass and favour natural regeneration has been recommended (Otsamo *et al.* 1995). However, the high cost of site preparation and planting seedlings for this type of restoration program is economically unattractive for large-scale application in tropical countries. Instead, forest rehabilitation and management systems are needed that simultaneously accelerate natural regeneration of species-rich native forest while also providing economically and socially valuable forest products (Parrotta *et al.* 1997). Our goal is to find a low-cost alternative to intensive mechanical site preparation and tree plantations initiated from nursery-grown seedlings for restoring productivity of *Saccharum*-dominated grasslands in Panama.

If seed source is a major limitation, planting desired species would improve natural regeneration. Once trees are established, they may act as regeneration nuclei by attracting vertebrate seed dispersers (Nepstad *et al*. 1990, Lamb *et al*. 1997) and providing favorable germination and growth microhabitats (Kellman 1985). Native tree species have been underutilized in tropical reforestation projects, despite their proven ability to grow successfully on degraded pastures (Gonzalez and Fisher 1994, Butterfield 1995, Butterfield and Espinoza 1995). In this study we planted seeds of twenty native tree species directly into the *Saccharum* to evaluate their germination, survival, and growth. Species with a range of shade-tolerance and seed size characteristics were chosen, including small-seeded pioneers and large-seeded, shade-tolerants, as well as a range in between (Bazazz and Pickett 1980, Augspurger 1984, Denslow 1987, Whitmore 1989). To test the hypothesis that *Saccharum spontaneum* is a major barrier to native tree establishment, we planted 15,000 seeds of these species in a factorial experiment, varying above- and below-ground *Saccharum* competition with four shading and mowing treatments. Two intensities of mowing were used to vary above-ground competition from the *Saccharum*, leaving roots and thus below-ground competition intact. Two levels of shading (75% and 95% of full sunlight) were used to decrease below-ground competition from the *Saccharum* while varying the levels of above-ground competition. Seedling performance may be affected by proximity to forested areas (Gonzales-Montagut 1996), so we utilized plots at three distances from the forest.

MATERIALS AND METHODS

Study site

Las Pavas (9°06' N, 79°53' W), Panama, is located 4 km southwest of the Barro Colorado Nature Monument, where the Smithsonian Tropical Research Institute research reserve is located. The Nature Monument supports tropical moist lowland forest, as did the adjacent study area prior to deforestation. Deforestation of the public lands between the Canal operating area and private landholdings began in approximately 1976 (Penna Franco 1990). By 1984 most of the forest had been cut, burned, and used for subsistence agriculture. Small farm lots were quickly abandoned, however, most likely due to declining productivity, and were subsequently invaded by *Saccharum spontaneum.* The entire area has moderately rolling topography, dissected by small streams that support corridors of native tree species; there are also a few tree islands 100-500 m in diameter in the *Saccharum*.

Rainfall on Barro Colorado Island averages 2600 mm, with a pronounced dry season from mid-December until mid-April (Windsor, 1990). Rainfall was above average during the first wet season of the study (1996) but well below average during the 1997 dry season (Smithsonian Environmental Sciences Project, *unpublished data*). Soils are oxisols (Cavelier 1992), with pasture soils characterized by moderate pH (mean 5.97), low total percent nitrogen (mean 0.34%), and moderate to low available phosphorous (mean 0.0065 mg/g). All other micro and macronutrients in the upper 10 cm of soil were found in concentrations not limiting to plant growth; aluminum and iron concentrations were well below toxic levels (Hooper *et al*. in prep.).

Sampling design

Five sites were chosen to represent a diversity of topographic conditions and were separated by 0.4 to 0.8 km. Each site was located in an area dominated by *Saccharum spontaneum* adjacent to a different tree island or riparian forest corridor which we refer to as a forest edge. To determine whether there was an effect of distance from these forest edges on tree species performance a transect perpendicular to each forest edge was extended into the *Saccharum*-dominated sites. Plots were placed at 10, 35, and 85 m along this transect. Each plot consisted of five subplots, each 1 x 8 m in size, for the five treatments: 1) mowing the *Saccharum* once, 2) mowing three times, 3) mowing three times and shading by 75%, 4) mowing three times and shading by 95%, 5) control: no mowing or shading. The two shading treatments were created by construction of a 1.5 m high frame that was placed 0.25 m outside the subplot perimeter and covered with one or two layers of polyurethane shade cloth that removed approximately 75% (mean 77%, range 73-86%) and 95% (mean 95%, range 93-98%), respectively, of incident solar radiation. The shade cloth was extended far enough down the sides of the frame to ensure that each entire subplot was shaded at all times. The subplots were separated by at least a 1-m pathway which was mown monthly to minimize *Saccharum* competition from both roots and shading. The shade houses were located 5 m from the three unshaded treatments so that the latter would not be shaded. *Saccharum* treatments were implemented by hand-cutting the *Saccharum* with machetes in July 1996, and again in November 1996 and March 1997 for those mown three times.

Species selection and planting

Twenty species of trees native to Panama were chosen to represent a diversity of families and shade-tolerance characteristics, and with approximately equal numbers of large-, mid-, and small-seeded species (Table 1). Species were chosen with the added constraint that, whenever possible, they have an established ethnobotanical use (Aguilar and Condit 2001). Seeds were collected from five trees from widely separated locations (A. Sautu, *unpublished data*). From each tree, 400 seeds were collected, and the seeds from all trees were pooled and mixed. Exocarps were removed, and seeds were planted within five days of collection for all species not known to have seed dormancy, and as soon as possible for the rest (Table 1). Seven-hundred-and-fifty seeds of each species were utilized in this experiment; the rest were utilized to evaluate each species' light-dependence by measuring germination rates under greenhouse conditions with varying levels of shade (A. Sautu, *unpublished data*).

Ten seeds from each species were planted in each 1 x 8 m subplot, for a total of 200 seeds per subplot; seeds were located randomly within each of these subplots. Randomization was introduced by construction of a grid with 20 cm subdivisions; location of each species within this grid was chosen by random draw. Seeds were planted between July 1996 and March 1997. Four censuses at two-month intervals (January, March, May, and July 1997) were performed, including height measurements of each seedling. Height measurements were recorded as distance from the soil surface to the apical meristem with a precision of 1 mm.

Impact of treatments on light, soil moisture, and Saccharum *biomass*

Light.—A Li-Cor photometer (quantum sensor) attached to a Datalogger (Li-Cor, Lincoln, Nebraska) was used to measure the photon flux density in the photosynthetically active range (PAR). Instantaneous readings were taken on cloudless days in May 1997 between 10:00 am and 2:00 pm at three heights above the ground: 3 m, 0.5 m (above the *Saccharum* litter), and 0.1 m. Two measurements were taken for each 1 m x 8 m subplot.

Saccharum *biomass*.—All live *Saccharum* tissue and all dead litter were collected in a 1 x 1 m quadrat in each subplot at the end of the experiment and also during the third mowing treatment (March, 1997) to calculate *Saccharum* growth. Samples were dried, and the dry mass recorded to the nearest gram.

Soil moisture.— Soil samples were taken from the top 10 cm at the center of each subplot within a 2-day period in May 1997, 7 days after the previous rainfall. Wet mass was recorded to the nearest milligram; samples were oven-dried at 60 °C for 2 days, and then re-weighed. Soil moisture was calculated as 100 (mg H_2O / mg dry soil).

Statistical Analyses: Overall effects evaluated using ANOVA

A two-way split-plot analysis of variance (ANOVA) was computed using the procedure GLM in SAS (SAS Institute 1988), with *Saccharum* biomass and light as response variables. The ANOVA model accounted for distance from the forest with three levels (10 m, 35 m, 85 m) as the main plot factor, treatment of the *Saccharum* with five levels (once mown, thrice mown, thrice mown and 75% shaded, thrice mown and 95% shaded, and control) as the sub-plot factor, and their interaction. Sites were considered a random factor, and we controlled for their effect by treating sites as statistical blocks. Tukey post-hoc analysis was performed on all variables found to be significantly ($P < 0.05$) affected by the factors.

Repeated-measures ANOVA following the same two-way split-plot design was computed to determine the effect of distance from the forest, *Saccharum* treatment, time, and their interactions on tree seedling germination, abundance, survival, mean height, and relative height growth in all unburned sites (n = 45). Tree seedling abundance was defined as the number of individuals alive per time period per subplot. Growth was defined as relative height growth (RHT), calculated as:

$$\mathrm{RHT} = [\ln (H_t) - \ln (H_{t-1})] \;/\; T$$

where H_{t-1} and H_t are measurements of heights on two consecutive dates, T is the number of days between these dates, and ln is the natural logarithm.

Statistical Analyses: Species-specific effects evaluated using multivariate analyses

Effect of treatment. —To understand the effect of treatments on each species, we used Redundancy Analysis (RDA: Rao 1964) in a MANCOVA-like procedure, as proposed by Verdonschot and ter Braak (1994). We chose RDA because the species variables in our data table could not be normalized, making the data unsuitable for standard MANCOVA procedures; RDA uses permutation testing to find the significance of explained variation and thus species abundances do not have to be normally distributed prior to analysis. In the present analysis, RDA was chosen instead of other multivariate procedures which use asymmetrical distance measures (measures which exclude 0) such as canonical correspondence analysis (CCA), because we planted a known number of individuals per species, thus making zeros a meaningful basis for comparison among sites (Legendre and Legendre 1998).

RDA was utilized to implement a three-way MANCOVA-like design to test the significance of the three main factors (distance from the forest, treatment of *Saccharum*, and time), as well as all two-way interactions, and the three-way interaction. Site and the interaction of site with all the main factors and interactions were used as covariables in order to treat site as a statistical block. Each main factor and each interaction was coded as a matrix of predictor dummy variables by site, much the same as in standard multiple regression with discrete independent variables except that the dummy variables were made orthogonal so that they would not be correlated to the covariables (Legendre and Anderson 1999). Analysis involved testing each main or interaction effect using 999 permutations in the program Canoco 4 (ter Braak and

Smilauer 1998), while controlling for the effect of the main factors, sites, and their interactions not included in a given test. To do this, the matrix of dummy variables by site for the factor of interest was utilized as the matrix of predictors, and all the other factors and interactions were placed in another matrix used as covariables in the analysis. This analysis was performed separately with the following response variable matrices: 1) germination and 2) relative height growth for all unburned sites ($n = 45$). As with all our multivariate analyses, post-hoc planned pairwise comparisons were computed using 999 Monte Carlo permutations, and significance judged after Bonferroni adjustment ($P < 0.05$ was considered significant).

Effect of fire.—A wildfire between census two (March) and three (May) burned two out of the five sites, so all previous analyses were performed on the three unburned plots. To test the effect of fire on germination and species abundance, a three-way MANOVA-like analysis using the dummy-variable coding method (detailed above) was performed. The three main factors included: distance from forest, treatment of the *Saccharum*, and fire (burned, unburned). This analysis was performed on two species matrices: 1) the number of individuals present for each species at 30 unburned and 30 burned subplots during the final July census (subplots for one unburned site were removed from the analysis to achieve a balanced design) and 2) the number of individuals germinating in these 60 subplots in July 1997.

Survival.—The effect of the treatments on species survival could not be tested in the same way as for the germination, abundance, and growth data because for survival data the symmetrical distance measure used in RDA was not appropriate. This is because, in the data matrix of survival of species by sites, it is impossible to differentiate a zero resulting from a lack of germination (inappropriate for evaluating survival) from a zero resulting from death after germination (appropriate). The survival data did not approach normality, and no transformation managed to achieve it; thus MANOVA could also not be used. Therefore, we used multiple regression procedures for each species separately, with survival as the response variable, using only the data for each site where a given species had germinated. To test the effect of treatment on survival, a matrix of dummy variables coding for the five treatments was utilized as the predictor variable, and statistical significance was analyzed using permutation testing, which does not require normality. The partial regression coefficients were used to assess the effect of the treatments on relative survivorship. To avoid over-specification of the model, the dummy variables coding for the 95% shaded treatment were removed.

Integrated performance index. —To assess the overall performance of each species in the *Saccharum* treatments, an integrated performance index was calculated (De Steven 1991). This performance index is calculated as the product of germination, survival, and growth. De Steven (1991) used mean height attained by tree seedlings as a measure of growth whereas we utilized relative height growth between May and July in order to standardize for differences in timing of emergence.

Index of light-dependence.—To evaluate species' light-dependence, relative proportional germination was calculated per species under greenhouse conditions with 3%, 30% and 50% incident light levels using seeds collected from the same seed sources (A. Sautu, *unpublished data*). A principal component analysis (PCA) was then conducted on these proportional values, and the first principal component was utilized as an index of light-dependence (Table 1).

RESULTS

Effect of treatment on Saccharum *growth, light levels, and soil moisture*

Both shading and mowing treatments significantly ($F_{[4,24]} = 57.7$, $P < 0.0001$) reduced live *Saccharum* biomass (Table 2). *Saccharum* growth rate was significantly ($F_{[3,24]} = 17.1$, $P < 0.0001$) reduced with shading, whereas it did not decrease with mowing ($P = 0.058$; once mown: 8.9 ± 1.5 g m^{-2} day^{-1}; thrice mown: 10.9 ± 1.7 g m^{-2} day^{-1}). Light levels in the photosynthetically active range (PAR) were significantly affected by *Saccharum* treatment (0.5 m: $F_{[4,24]} = 15.6$, $P < 0.0001$; 0.1 m: $F_{[4,24]} = 3.2$, $P = 0.029$). PAR at 0.5 m above-ground did not significantly differ when once mown or 75% shaded, averaging 14 -15% of incident solar radiation. PAR also did not significantly differ between the control and 95% shaded *Saccharum*, averaging 3-5% incident solar radiation. Soil moisture ranged from 56.3 ± 4.2% when 75% shaded and thrice mown to 42.0 ± 3.6% when thrice mown.

Overall effect of distance from the forest on tree seedling performance

Neither distance from the forest nor the interaction of distance from the forest with time or treatment had any significant effect upon tree seedling germination, abundance, survival, or growth.

Overall effect of Saccharum *treatment on tree seedling performance*

Germination, survival and mean height of tree seedlings were significantly ($F_{[4,24]} = 11.7$, $P = 0.003$; $F_{[4,24]} = 2.8$, $P = 0.040$; $F_{[4,24]} = 3.9$, $P = 0.004$ respectively) affected by *Saccharum* treatment; all were higher when the *Saccharum* was artificially shaded in comparison to the control (Table 3). In contrast, mowing the *Saccharum* three times yearly led to the lowest germination, survival, and mean height. Percentage germination, survival and mean height nearly doubled when the *Saccharum* was mown three times and shaded in comparison to when it was mown three times (germination rose from 13% to 23%, survival from 39% to 79%, and mean height from 5.5 cm to 9.7 cm). Mowing the *Saccharum* once led to intermediate germination, survival, and mean height, which were not significantly different from these extremes. Relative height growth (RHT) was also affected by treatment ($F_{[4,24]} = 4.9$ $P < 0.010$), but this effect was only significant in the early dry season ($F_{[4,24]} = 3.5$, $P = 0.025$). Height growth was an order of magnitude higher in both shaded treatments than in the unshaded treatments. In both the *Saccharum* control and the thrice mown treatment, growth was negative in the dry season, indicating that increments resulting from growth could not match losses.

The interaction of time and *Saccharum* treatment significantly affected abundance ($F_{[4,24]} = 13.0$, $P = 0.003$; Fig. 1). In January, after the wet season, tree seedling abundance did not differ among the treatments. In contrast, during the dry season, lower germination and survival in the unshaded treatments led to a significantly lower abundance of tree seedlings by May in the unshaded *Saccharum* compared to the shaded. Mean abundance decreased during the early dry season in both the *Saccharum* control and the unshaded, thrice mown *Saccharum.* At the final census, in the shaded *Saccharum* (75% and 95%) tree seedling abundance was over double that found in the unshaded, thrice mown *Saccharum*.

Time significantly affected germination ($F_{[4,24]} = 36.3$, $P < 0.001$) and seedling height ($F_{[4,24]} = 3.2$, $P = 0.005$) (Appendix 1). Germination was higher in the wet seasons (January: 5.2 ± 1.1%; July: 6.4 ± 0.9%) than in the dry season (March: 2.0 ± 0.4%; May: 3.7 ± 0.8%). Mean seedling height was highest in the July wet season (9.7 ± 0.5 cm) and lowest in the late dry season (May: 5.6 ± 0.5 cm).

Overall effect of fire

Fire significantly ($P < 0.001$) lowered germination and survival. Following fire, mean germination was 5.3%, while the mean in all unburned plots was 17.3%. Mean survival (via resprouting) was 6.7% in burned plots, whereas survival in unburned plots averaged 57.2%.

Species- specific effects

Large-seeded, shade-tolerant species had the highest germination and survival in the *Saccharum* control (Table 4). Germination correlated positively with seed size ($P < 0.001$): *Trema* and *Annona*, both with seeds weighing less than 0.1 g, had the lowest mean germination (3-7%), while *Calophyllum,* which had an average seed size of 14 g, had the highest germination (42%). Survival also correlated positively with seed size ($P = 0.002$). Survival was so low for two small-seeded species (*Annona* and *Trema*) that they could not be considered in the remaining survival analyses. Survival in the *Saccharum* control correlated negatively with the index of light-dependence ($P = 0.028$), and positively with seed size ($P = 0.058$) suggesting that large-seeded, shade-tolerant species had higher survival in the uncut *Saccharum.*

Germination

Effect of Saccharum *treatment.* —The germination of all species varied depending upon *Saccharum* treatment and time (RDA time x treatment interaction: $F_{[12,24]} = 1.8$, $P = 0.005$). The effect of treatment was only significant during the dry season (March: $P = 0.001$; May $P = 0.002$). These differences were pronounced enough that a significant ($P < 0.001$) effect of *Saccharum* treatment on germination over all time periods was found. This is illustrated by the ordination of the matrix of overall germination per subplot (Fig. 2). The first axis (horizontal) explained most of the species variation. It correlated positively with germination in both the 75%

and 95% shaded treatments, and negatively with germination in the unshaded treatments. This is indicated by the position of the treatment vectors in the ordination; both levels of shading are found on the right side of the ordination, and all the unshaded treatments are located on the left. Germination did not significantly differ with the level of shading or with the level of mowing. Thus, species' germination varied depending upon the presence or absence of shading, but was not affected by mowing.

The species most affected by the difference between the shaded and unshaded *Saccharum* formed two polarized clusters in this ordination space, represented by their positions along the first ordination axis (Fig. 2). Species in the first cluster had high germination where the *Saccharum* was shaded, especially *Genipa*, *Ormosia*, *Dipteryx*, *Posoqueria*, and *Heisteria.* The high correlation between germination of these species and shading is represented in the ordination by the low angle of their vectors in relation to the first axis, and the high length of their vectors. They had 15-40% higher germination in shade compared to the control, and approximately 10% less germination in the thrice mown treatment compared to the control (Fig. 3). The second species group, comprised of *Byrsonima* and *Sterculia* had the opposite response (Fig. 2); both species had higher germination in the unshaded, thrice mown treatment. The germination of *Sterculia* doubled, while *Byrsonima* had over 9 times higher germination in the thrice mown treatment compared to the shaded treatments (Fig. 3). The very small-seeded species (*Annona*, *Jacaranda*, *Trema* and *Vochysia*) had highest germination in the 75% shaded treatment (Figs. 2 and 3). Species that germinated in the wet season (*Calophyllum*, *Virola*, and *Spondias*) were indifferent to the ordination axis, illustrated by their high angle from the first ordination axis, and the short length of their vectors (Fig. 2).

This ordination also suggests that it is not light levels that caused differential germination in relation to the gradient in shading (Fig. 2). Germination significantly differed between the uncut *Saccharum* control and the 95% shaded treatment (P = 0.014; RDA post-hoc analysis), but light levels (PAR) did not differ significantly between these treatments. Similarly, germination was significantly different between the 75% shaded and once mown treatment (P = 0.011), but no significant difference existed between PAR in these two treatments.

Effect of fire.—When burned, most species germinated poorly (RDA; P < 0.001). *Dipteryx*, *Hampea*, *Heisteria*, and *Sterculia* had germination rates approximately cut in half following fire, while *Posoqueria* and *Genipa* were very sensitive to fire (6.3% germinated on burned and 42.4% on unburned sites in the former, 7.3% and 39.5% in the latter). *Spondias* had only slightly lower germination on unburned sites. *Trema* and *Byrsonima* had the opposite response to fire, with *Trema* averaging 3.6% germination on burned sites and 2.2% on unburned, and *Byrsonima* 7.6% on burned and 7.0% on unburned sites. Other species could not be evaluated because they germinated before the wildfire.

Survival

Effect of Saccharum *treatment*.— The survival of all species except *Genipa* was highest in at least one of the shaded *Saccharum* treatments (Fig. 4). Most species had lower survival in the thrice mown treatment relative to the control, but *Spondias* and *Sterculia* were opposite. Survival when the *Saccharum* was mown once was intermediate, and similar to the control for most species, except *Jacaranda*, *Genipa*, *Spondias* and *Sterculia*, which had over double the percentage survival when the *Saccharum* was mown once compared to the control.

Effect of fire.—Species varied in their ability to survive fire. Most died, but five of the larger-seeded species were able to resprout. Their survival ranged from 20.2% for *Ormosia* to 2.2% for *Calophyllum* and *Virola*; *Carapa* and *Dipteryx* also resprouted.

Growth

Effect of Saccharum *treatment.*— Species varied in their relative growth rate in relation to treatment and season (RDA time x treatment interaction; $F_{[4,8]} = 2.9$, $P < 0.001$). Ordinations performed on the species matrix of relative height growth by subplots produced biplots in which most of the species variation was explained by the first axis (horizontal) in both the wet season (Fig. 5) and dry season (Fig. 6). In the dry season, the first axis positively correlated with growth in both the 75% and 95% shaded treatments, but there was no association with mowing. All species in the dry season had higher growth in the shaded treatments (Fig. 5). In the wet season, both mowing and shading had an effect upon species' growth. The first axis of the ordination correlated with the presence or absence of shading. Many species with low growth in the control and thrice mown treatments achieved high growth in the shaded treatments, especially those with small- to mid-sized seeds (*Jacaranda*, *Posoqueria*, *Heisteria*, *Genipa*, and *Hampea).* A second axis appears to represent a light gradient: both treatments with the lowest light levels (95% shaded and control) were positively correlated with this axis, and the treatments with higher light levels were negatively correlated with this axis. Most species had low growth when the *Saccharum* was mown three times except *Byrsonima, Sterculia*, *Dipteryx (*which achieved their highest growth rates in this treatment) and *Spondias.*

Overall performance: Integrated performance index

Ormosia had the highest integrated performance in the *Saccharum* control, coupling high growth with moderate survival and germination (Table 5). The large-seeded *Virola*, *Carapa*, and *Dipteryx* ranked next, with moderate germination and growth, and high survival. *Sterculia* had relatively high performance in the *Saccharum* control despite low germination because of its high growth rate. *Calophyllum* followed these with high germination, but low survival and growth. All other species had relatively poor performance in the *Saccharum* control.

Most species had much higher performance where the *Saccharum* was shaded, resulting from higher germination, survival, and growth, compared to the control. Germination and survival were similar for most species under both levels of shading, but performance in the 75% and 95% shaded treatments varied because growth differed. Generally, shade-tolerant species performed better in the 95% shaded *Saccharum*, whereas *Carapa*, *Dipteryx*, and *Jacaranda* had higher performance when the *Saccharum* was 75% shaded.

For most species, performance was low when the *Saccharum* was mown three times, except for *Byrsonima*, *Spondias,* and *Sterculia*. *Byrsonima* had zero performance in all other treatments, indicating its narrow tolerance of shaded conditions. In contrast, *Spondias* performed better when the *Saccharum* was 95% shaded and generally had high performance in all treatments except the control, indicating its range of tolerance.

DISCUSSION

Our results show that the invasive grass, *Saccharum spontaneum*, negatively affects germination, survival, and growth of native tree seedlings in abandoned Panamanian farmland. Most tree species showed a similar response to treatments that reduced *Saccharum* biomass. Their germination, survival and growth were significantly higher when the *Saccharum* was shaded in comparison to unshaded control conditions. Shading treatments essentially eliminated the *Saccharum*, and we presume that below-ground constraints were consequently reduced. Given that understory light levels were similar when the *Saccharum* was 95% shaded as in the control, we conclude that below-ground constraints were responsible for the large decrease in seedling performance when the *Saccharum* was present. In Amazonian pastures, Nepstad (1989) found that root competition from pasture grasses was a major limitation to tree seedling growth. He used trenching experiments to ascertain the effect of below-ground competition; we also recommend trenching experiments to clarify the effect of below-ground competition at our site in relation to other possible below-ground constraints such as allelopathy or soil factors. But our objective in the present experiment was to focus on treatments such as mowing and shading which are easier to implement and thus feasible in local reforestation projects.

Mowing the *Saccharum* three times exposed tree seedlings to high irradiance, which increased temperatures by 5-9°C, decreased humidity 10-15%, and lowered soil moisture by approximately 10% in comparison to the shaded treatments. We note that these values are approximate and may differ when larger areas are mown. *Saccharum* growth was undiminished with mowing. Tree seedling germination, growth, and survival were lowest under these conditions (approximately half those recorded in the shaded treatments). Other studies of tree regeneration in neotropical pastures have produced similar results. Gerhardt (1996) found that germination of *Swietenia macrophylla* was lowest in pasture mown three times yearly in comparison to unmown pasture, especially during the dry season. Many authors have found that tree seedlings in the neotropics have higher performance under the shade of pasture trees and shrubs because of protection from irradiation Uhl (1987), higher soil moisture (Kellman and Miyanishi 1982, Guevara *et al.* 1986, Vieira *et al*. 1994), and decreased root competition with grasses (Nepstad 1989).

We suggest that dry-season water stress, as a result of the dense *Saccharum*, limits tree seedling regeneration. Elimination of the *Saccharum* through shading significantly improved most tree species' germination and growth during the dry season. Previous research has shown that high temperatures and lower moisture availability in tropical pastures, compared to forest, resulted in water stress and limited seedling establishment and survival. Pasture grasses significantly decrease soil moisture availability because of their dense root mass in the upper 50 cm of soil (Uhl 1987, Nepstad *et al.* 1990).

Although these were the general trends, species were not identical in their response to mowing and shade, and species differences are important because they offer management options for different reforestation settings. Because species differences in response to experimental treatments were consistently predicted by seed size and shade-tolerance, we find it useful to group species using these characteristics when interpreting our results.

We first consider the species with the smallest seeds, *Trema*, *Annona*, *Vochysia* and *Jacaranda*. They had the lowest overall germination and survival, and their germination was highest when the *Saccharum* was 75% shaded but much lower with 95% shade, suggesting that they are light-dependent, as they are on Barro Colorado Island (Welden *et al.* 1991). Survival of these small-seeded species was very low in the unshaded treatments, suggesting that below-ground constraints also limit their success in the *Saccharum*. Survival and germination were lowest during the dry season, suggesting that competition for moisture may also be important. Nepstad (1989) found that small-seeded, light-demanding species (including *Jacaranda copaia*) had poor survival in Amazonian pastures because of low soil moisture (Nepstad *et al.* 1990). It has been suggested that these pioneer species hold the most promise for use in reforestation because of their fast growth and abundant regeneration in secondary succession (Finegan 1992, Condit *et al.* 1993). In abandoned farmland in Panama, however, they tolerate neither above- nor below-ground constraints imposed by the *Saccharum* and thus cannot be used.

For the next group, we consider three species that had high performance in the exposed conditions of the thrice mown *Saccharum* treatment and low performance in the *Saccharum* control. These are the savanna specialist *Byrsonima crassifolia* and the gap-colonists *Spondias mombin* and *Sterculia apetala* (Kellman and Miyanishi 1982, Condit *et al.* 1993). All three were light-demanding (Index of light-dependence > 0.2) and had large seeds (1 to 10 g). Germination rates for these species were never high, but for *Byrsonima* and *Sterculia* they were highest in the thrice mown treatment. In contrast to all other species, they had high survival and growth when the *Saccharum* was mown three times; in fact *Byrsonima* only survived in this treatment, and its growth rate was over twice that of any other species. We conclude that these species are able to tolerate dry, exposed conditions as well as below-ground constraints imposed by the *Saccharum;* their natural regeneration was limited by above-ground constraints, namely light. In addition, both *Byrsonima* and *Spondias* were able to germinate successfully after fire. Both species are found frequently in these fire-prone grasslands.

Third, we consider a group of three species – *Posoqueria*, *Genipa*, and *Heisteria* – which had the opposite response to *Saccharum* treatment as the previous light-demanding group. They had small seeds (0.1 to 1 g) but were shade-tolerant, with high germination in the shaded treatments and low germination in the mown treatments. They had negative indices of light-dependence, indicating shade-tolerance as well (Table 1). Since shade did not limit their performance, we conclude that below-ground constraints resulting from *Saccharum* competition must have.

The large- to very large-seeded (2.9 to 50.4g) species form the final group. They ranged from the moderately shade-tolerant *Dipteryx* (Index of light-dependence –0.4, Table 1) to the very shade-tolerant *Calophyllum*, *Carapa*, and *Virola* (Index of light-dependence < –0.9). The latter three germinated immediately upon planting (in the wet season), irrespective of *Saccharum* treatment, and despite slow growth rates, they were relatively tall (>10 cm) by the final census.

In contrast, *Dipteryx* had dormant seeds and did not germinate until the dry season, grew best in the treatments with higher light, and showed shade-dependence in germination. All four large-seeded species had high survival and relatively high performance in the *Saccharum* control (Table 4). We conclude that the *Saccharum* did not completely limit their regeneration. A reforestation effort starting with seed and minimal pre-sowing treatment is only likely to succeed with these large-seeded, shade-tolerant species.

Fires burn yearly in the dry season in these *Saccharum*-dominated grasslands, and our data show that these wildfires are also a major barrier to tree regeneration. Fire killed most species and significantly lowered the germination of all except *Trema* and *Byrsonima* (but those two cannot compete with established *Saccharum*). Resprouting from cut stems or stumps is a very common mechanism for reestablishment following disturbance (Aide *et al.* 1995), and we found that seedlings of several large-seeded species (*Carapa*, *Dipteryx*, *Virola*, *Ormosia*, and *Calophyllum)* could resprout following fire. Recurring fires, as a result of grass invasion following pasture abandonment, arrest natural tree regeneration in abandoned pastures at other neotropical sites as well (Janzen 1988, Nepstad *et al.* 1991, Aide and Cavelier 1994).

Management suggestions

Fire is a major barrier to tree regeneration at our sites, limiting both establishment and species diversity. We therefore recommend the establishment of firebreaks, which have also been an integral part of reforestation strategies in Costa Rica (Janzen 1988) and the Amazon (Nepstad *et al.* 1990). The breaks must be large for effective fire protection because the flame height of *Saccharum* wildfires can reach over 15 m.

Many alternatives have been suggested for forest restoration throughout the wet tropics. These range, in order of increasing cost, from simply allowing natural regeneration to proceed, to planting seeds or seedlings to assist natural regeneration, through establishing tree plantations and allowing recruitment of tree seedlings below them (Brown and Lugo 1994, Kuusipalo *et al.* 1995, Guariguata *et al.* 1995). Our goal was to find a low-cost strategy for extensive forest restoration in abandoned Panamanian farmland, and our results suggest that even with the removal of fire, natural tree regeneration will not proceed unassisted because the *Saccharum* poses a formidable barrier to the small-seeded species that have the highest probability of being dispersed (eg. Nepstad *et al.* 1996). In general, tree seedling performance was lowest in the thrice mown treatment, and not significantly different between the unmown and once mown *Saccharum*. We therefore do not recommend mowing as a site treatment. Shade greatly enhanced the performance of most tree species and effectively killed the *Saccharum*. Producing a shade cover as quickly as possible is therefore the best strategy for reforestation. We thus suggest planting large-seeded tree species (both the moderately and highly shade-tolerant) directly into the *Saccharum* to catalyze forest regeneration because our data suggest that they can survive in the *Saccharum*. The shade-tolerant species are advantageous because they have immediate and high germination, whereas the more light-demanding species have higher growth.

In the Brazilian Amazon, Knowles and Parrotta (1995) also found that large-seeded species could be propagated most efficiently by direct seeding. One limitation of using large-seeded species, however, is that their seeds generally have limited viability, and must be planted as soon as possible after collecting. Once a shade cover is produced, we therefore suggest planting seeds of the smaller-seeded, shade-tolerant species (*Posoqueria*, *Genipa*, and *Heisteria*) to increase species richness. Their high performance in shaded conditions where the *Saccharum* was absent suggest that they would perform well, and their longer seed survival and small seed size are advantageous for collecting and planting. Also, these species could be planted directly under isolated trees, shrubs, and clumps of *Musa* found in these *Saccharum*-dominated grasslands, as tried by Vieira *et al.* (1994) in Amazonian pastures.

Successful reforestation strategies at other sites such as the Brazilian Amazon (Knowles and Parrotta 1995) and South-East Asia (Otsamo et al. 1995) have involved deep-ripping of the soil and planting wildlings or nursery-grown seedlings. At our sites, soil trenching would expose the soil to erosion and introduce high site preparation costs. We do not recommend planting seedlings directly into the *Saccharum* because it is so dense that it would damage the seedlings. However, given that firebreaks must be established, we recommend that species of local value be planted as seedlings in the firebreaks. We also recommend direct seeding of the colonizing species *Byrsonima* and *Spondias* in the firebreaks, where they could benefit from the mowing treatments undertaken for fire prevention. Both species performed well in dry, exposed conditions, and both have long-lived seeds which are easy to manipulate and store. Given that site access is difficult in the *Saccharum*, planting these species in the cleared areas would be simple and cost-effective. Once established, these species could act as a green firebreak and attract frugivores, increasing seed dispersal to the regeneration area, as has been found for windbreaks in Costa Rica (Harvey 2000).

Our results suggest that indigenous botanical diversity can help provide a range of cost-effective reforestation strategies in *Saccharum*-dominated grasslands. A knowledge of species performance under shaded, exposed, and control conditions is critical for matching the most promising species to site characteristics, thus maximizing their reforestation potential. Another barrier that we cannot address is the implementation of reforestation. Demonstration of the economic and ecological benefits of forest restoration on degraded land is the next necessary step.

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TABLE 1. Twenty species of native trees indigenous to Panama planted in the experiment. Throughout the text, species are referred to by their generic names.

Species	Family	Species Code	Seed Mass (g)	Index of Light-Dependence†	Dispersal Agent‡	Date Collected (mm/dd/yr)	Date Planted (mm/dd/yr)	Germination†† Date
Annona spraguei	Annonaceae	Annosp	0.04	0.831	animal	09/20/96	09/26/96	1
Antirrhoea trichantha	Rubiaceae	Antitr	0.02		bird	08/02/96	08/18/96	
Byrsonima crassifolia	Malphigiaceae	Byrscr	2.08	0.998	animal	07/15/96	08/07/96	3
Calophyllum longifolium	Guttiferae	Calolo	13.70	–0.934	bat	08/27/96	09/01/96	1
Carapa guianensis	Meliaceae	Caragu	50.36	–0.991	animal	10/25/96	10/29/96	1
Ceiba pentandra	Bombacaceae	Ceibpe	0.52		wind	01/10/97	01/15/97	
Dipteryx panamensis	Fabaceae	Diptpa	16.66	–0.379	animal	01/12/97	01/13/97	2
Genipa americana	Rubiaceae	Geniam	0.14	–0.783	animal	02/08/97	02/11/97	2
Hampea appendiculata	Malvaceae	Hampap	0.21	0.146	animal	01/15/97	01/19/97	3
Heisteria concinna	Olacaceae	Heisco	0.30	–0.966	animal	03/06/97	03/08/97	3
Jacaranda copaia	Bignoniaceae	Jac1co	0.01	0.044	wind	09/10/96	09/26/97	1
Lindackeria laurina	Flacourtiaceae	Lindla	0.09		animal	08/01/96	08/07/96	

Ormosia macrocalyx	Fabaceae	Ormoma	0.48	0.619	animal	08/15/96	09/06/96	1
Posoqueria latifolia	Rubiaceae	Posola	0.62	–0.992	animal	01/08/97	01/13/97	2
Spondias mombin	Anacardiaceae	Sponmo	2.18	0.999	animal	08/15/96	08/21/96	1
Sterculia apetala	Sterculiaceae	Sterap	1.28	0.215	animal	01/27/97	01/31/97	3
Trattinickia aspera	Burseraceae	Tratas	0.19		animal	10/28/96	11/23/96	
Trema micrantha	Ulmaceae	Tremmi	0.01	–0.111	bird	08/02/96	09/04/96	1
Virola surinamensis	Myristicaceae	Virosu	2.89	–0.964	animal	07/02/96	07/09/96	1
Vochysia ferruginea	Vochysiaceae	Vocyfe	0.02	0.913	wind	10/10/96	10/14/96	1

Notes:

†Index of light-dependence is the first PCA score of proportional germination data under varying light levels in greenhouse conditions (A. Sautu, *unpublished data*); it is left blank for the species that did not germinate during the experiment. Scores ranged from –0.99 (shade-tolerant) to 0.99 (light-demanding).

‡ animal = animal dispersal, wind = wind dispersal, bat = dispersal primarily by bats, bird = dispersal primarily by birds.

††1 = January 1997, 2 = March 1997, 3 = May 1997. Four species did not germinate and are consequently left blank. They did not germinate in the field or in greenhouse trials suggesting that their seed viability was low (A. Sautu, *unpublished data*).

TABLE 1 continued

Table 2. Effect of the treatments on *Saccharum*, light (PAR) at 0.5 m above-ground, percent incident solar radiation (I) and our interpretation of above-ground and below-ground constraints imposed by the *Saccharum* under each treatment.

	Biomass (g)		Growth Rate†		Light‡			Constraints	
Treatment	mean	stderr	mean	stderr	mean	stderr	I	above-ground	below-ground
Control	4652^a	1134			39^c	14	3%	high	high
Once mown	3205^a	523	8.9^a	1.5	215^b	95	15%	low	high
Thrice mown									
Not shaded	1308^b	205	10.9^a	1.7	550^a	89	39%	low	high
75% shaded	179^c	60	1.5^b	0.5	201^b	35	14%	low	low
95% shaded	38^d	10	0.3^c	0.1	70^c	20	5%	high	low

Notes:

Similar superscripts indicate no significant ($P < 0.05$) difference according to Tukey post-hoc analysis. *Saccharum* biomass was natural log (ln) transformed, and light levels were ln (x + 0.1) transformed.

† grams m^{-2} day^{-1}

‡ μmoles m^{-2} sec^{-1}

TABLE 3. Effect of *Saccharum* treatment on tree seedling performance: percentage germination, percentage survival, mean seedling height (Height), and dry-season (March-May 1997) relative height growth.

Treatment	% Germination†		% Survival‡		Height (cm)		Relative Height Growth (day^{-1})	
	mean	stderr	mean	stderr	mean	stderr	mean	stderr
Control	14.06^{bc}	1.7	44.23^{b}	9.8	7.34^{b}	0.54	$–0.00009^{b}$	0.00029
Once mown	17.22^{abc}	1.4	62.30^{ab}	7.6	6.75^{bc}	0.45	0.00027^{b}	0.00027
Thrice mown								
Not shaded	12.95^{c}	1.2	39.00^{b}	6.6	5.47^{c}	0.53	$–0.00038^{b}$	0.00118
75% shaded	23.11^{a}	1.2	74.13^{a}	5.2	9.70^{a}	0.57	0.00235^{a}	0.00022
95% shaded	19.45^{ab}	1.9	78.92^{a}	5.4	9.14^{a}	0.52	0.00210^{a}	0.00042

Notes:

Similar superscripts indicate no significant difference ($P < 0.05$) according to Tukey post-hoc analysis.

† square-root transformed: sqrt (x + 0.01)

‡ % survival was defined as: (number of individuals that germinated up to and including the May census which survived until the end of the experiment / number of individuals that germinated up to and including the May census)

TABLE 4. Percentage germination (% G) and percentage survival (% S) of all seeds planted in the uncut *Saccharum* control, grouped into 3 seed size classes, and 3 shade-tolerance classes.

		Pioneer†		Gap-dependent‡		Shade-tolerant††	
Size class	Seed size (g)	% G	% S	% G	% S	% G	% S
Small	< 0.15	12.8	35	5.0	0	21.0	0
Medium	0.15 to 1.0			16.1	64	21.1	5
Large	> 1.0	8.3	40	21.1	62	30.7	72

Notes:

† Pioneer (index of light-dependence > 0.75)

‡ Gap-dependent (index of light-dependence 0.75 to –0.75)

†† Shade-tolerant (index of light-dependence < –0.75)

TABLE 5. Integrated performance index (De Steven 1991) for each species, calculated as: (percentage germination x percentage survival x relative height growth). Percentage germination (G), percentage survival (S), Relative height growth x 10 $^{-3}$ (day^{-1}) between May and July (RHT) and the performance index (Index) are presented for each species, in each treatment, and listed in descending order in relation to performance in the *Saccharum* control. If no value for survival is given when a germination percentage is listed, that species did not germinate until the final census (July 1997). If a species did not germinate, the columns corresponding to that treatment were left blank. The shaded treatments were also thrice mown.

	Control				95% shaded				75% shaded				Thrice mown				Once mown			
Species	G	S	RHT	**Index**	G	S	RHT	**Index**	G	S	RHT	**Index**	G	S	RHT	**Index**	G	S	RHT	**Index**
Ormoma	30	64	3.65	**7.0**	48	97	4.53	**21.1**	61	82	3.60	**18.0**	19	27	3.39	**1.7**	43	68	2.28	**6.6**
Caragu	27	77	2.98	**6.2**	24	95	1.56	**3.6**	46	79	2.34	**8.5**	21	74	1.02	**1.6**	23	86	0.90	**1.8**
Virosu	24	80	3.05	**5.9**	26	96	4.79	**12.0**	20	82	1.26	**2.1**	19	0		**0.0**	27	67	0.40	**0.7**
Diptpa	32	74	2.41	**5.7**	43	94	2.59	**10.5**	49	89	2.59	**11.3**	24	54	6.41	**8.3**	36	67	4.80	**11.6**
Sterap	10	50	6.85	**3.4**	3	100	4.05	**1.2**	6	100	5.05	**3.0**	14	60	7.60	**6.4**	9	100	4.48	**4.0**
Calolo	41	60	1.07	**2.6**	41	95	3.79	**14.8**	36	84	3.73	**11.3**	43	22	0.16	**0.2**	49	69	1.59	**5.4**
Sponmo	14	40	3.33	**1.9**	27	100	12.85	**34.7**	24	60	8.02	**11.5**	24	80	8.34	**16.0**	34	100	3.20	**10.9**
Annosp	7	50	4.18	**1.5**	6	50	3.37	**1.0**	13	0		**0.0**	2	0		**0.0**	8	0		**0.0**
Vocyfe	19	20	2.90	**1.1**	17	43	3.52	**2.6**	20	27	–5.50	**–3.0**	7	0		**0.0**	8	25	–2.40	**–0.5**

Posola	34	50	0.15	**0.3**	50	63	5.13	**16.2**	62	64	2.13	**8.5**	24	40	0.48	**0.5**	41	25	10.31	**10.6**
Geniam	21	0		**0.0**	66	77	6.54	**33.2**	68	64	6.77	**29.5**	13	33	1.82	**0.8**	30	86	8.28	**21.4**
Jac1co	8	0		**0.0**	6	40	13.95	**3.1**	20	50	13.55	**13.6**	9	0		**0.0**	9	33	3.66	**1.1**
Tremmi	2	0		**0.0**					9	80	5.93	**4.3**	2	0		**0.0**	2	0		**0.0**
Heisco	8				20	100	8.48	**17.0**												
Byrscr	2												27	63	17.10	**28.7**				
Hampap	2				9	100	7.42	**6.7**												

TABLE 5 continued

Figure captions

Fig. 1. Effect of *Saccharum* treatments on mean percentage abundance (abundance / number planted) with the standard error, over all time periods. Similar lower case letters indicate that percentage abundance was not significantly different (Tukey post-hoc analysis, $P < 0.05$).

Fig. 2. Ordination biplot illustrating the significant ($P < 0.001$) effect of *Saccharum* treatment on species germination over all time periods. Similar superscripts indicate no significant difference ($P < 0.05$) following post-hoc analysis (planned comparisons). *Saccharum* treatment explained 22.8% of the species variation in germination. Biplot scores are represented following Type II scaling (correlation biplot). Arrows indicate treatments, and lines indicate species vectors. Species codes are listed in Table 1.

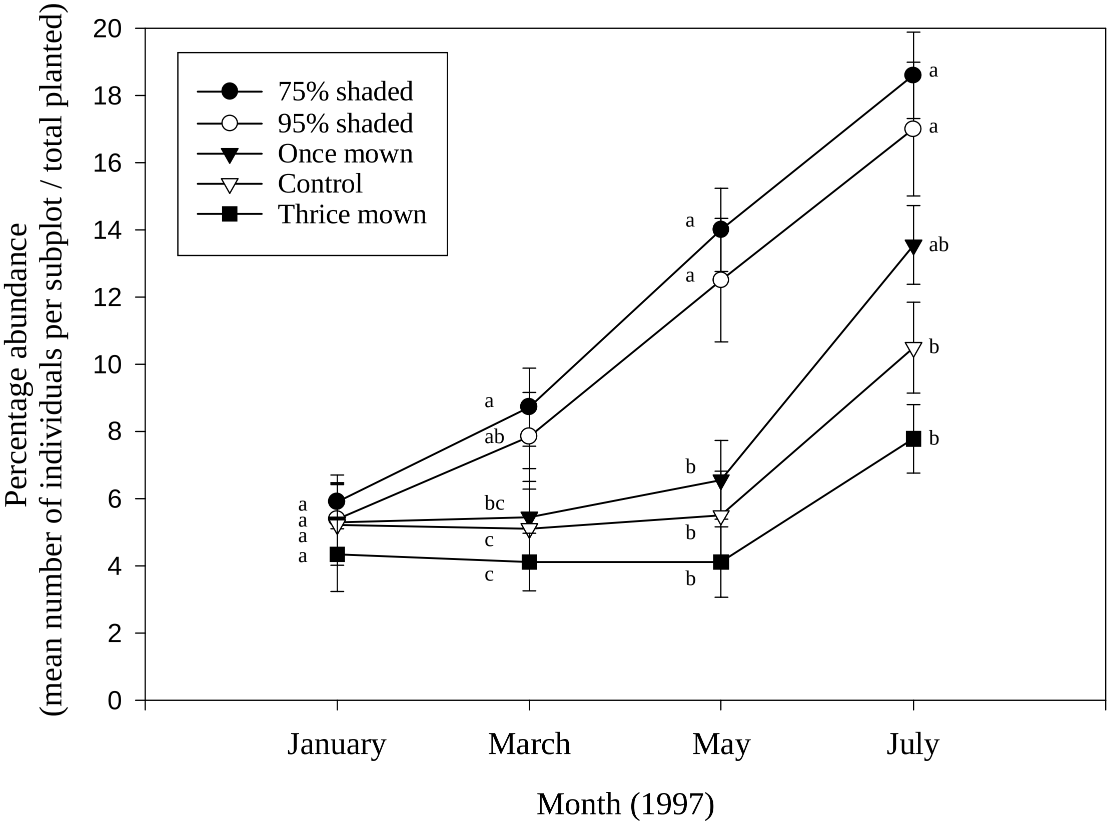
Fig. 3. Percentage germination in the *Saccharum* treatments vs. control for the 16 species that germinated. Species codes are listed in Table 1.

Fig. 4. Percentage seedling survival in the *Saccharum* treatments vs. control for the 11 species we were able to evaluate. Species codes are listed in Table 1. Cases where survival differed significantly ($P < 0.05$) from the 95% shaded treatment are marked with an asterisk. If the asterisk is located on the x axis, without a symbol, survival in the control significantly differed from the 95% shaded treatment.

Fig. 5. Ordination biplot illustrating the significant ($P = 0.002$) effect of *Saccharum* treatment on the relative height growth (RHT) of 11 tree species in the dry season, between March and May, 1997 (the other species had not yet germinated). Similar superscripts indicate no significant difference ($P < 0.05$) following post-hoc analysis. *Saccharum* treatment explained 24.1% of the species variation. The first and second axes

explained 15.4% and 5.6% respectively of the species variance. Arrows indicate treatments, and lines indicate species vectors. The codes associated with each species are listed in Table 1 and the symbols representing light requirements and seed sizes match Fig. 2.

Fig. 6. Ordination biplot illustrating the significant ($P < 0.001$) effect of *Saccharum* treatment on the relative height growth (RHT) of 16 tree species in the wet season, between May and July, 1997. Similar superscripts indicate no significant difference ($P < 0.05$) based on post-hoc analysis. *Saccharum* treatment explained 19.8% of the variance between species, with the first and second axes explaining 11.2% and 4.5% respectively. Arrows indicate treatments, and lines indicate species vectors. The codes associated with each species are listed in Table 1 and the symbols match Fig. 2.



Percentage abundance
(mean number of individuals per subplot / total planted)
20
18
16
14
12
10
8
6
4
2
0
January
March
May
July
Month (1997)
75% shaded
95% shaded
Once mown
Control
Thrice mown
a
a
a
a
a
ab
bc
c
c
a
a
b
b
b
a
a
ab
b
b

Fig. 1.

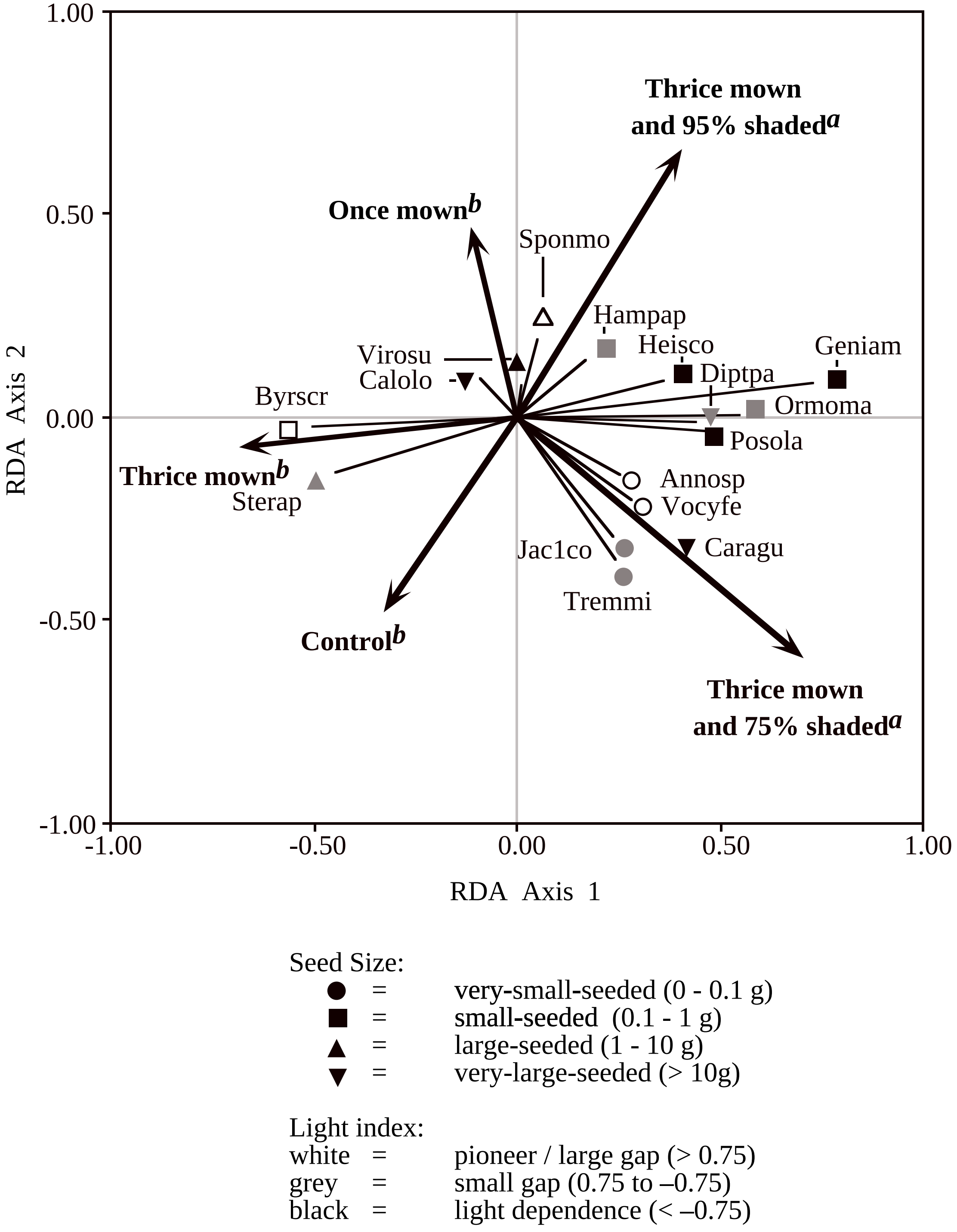
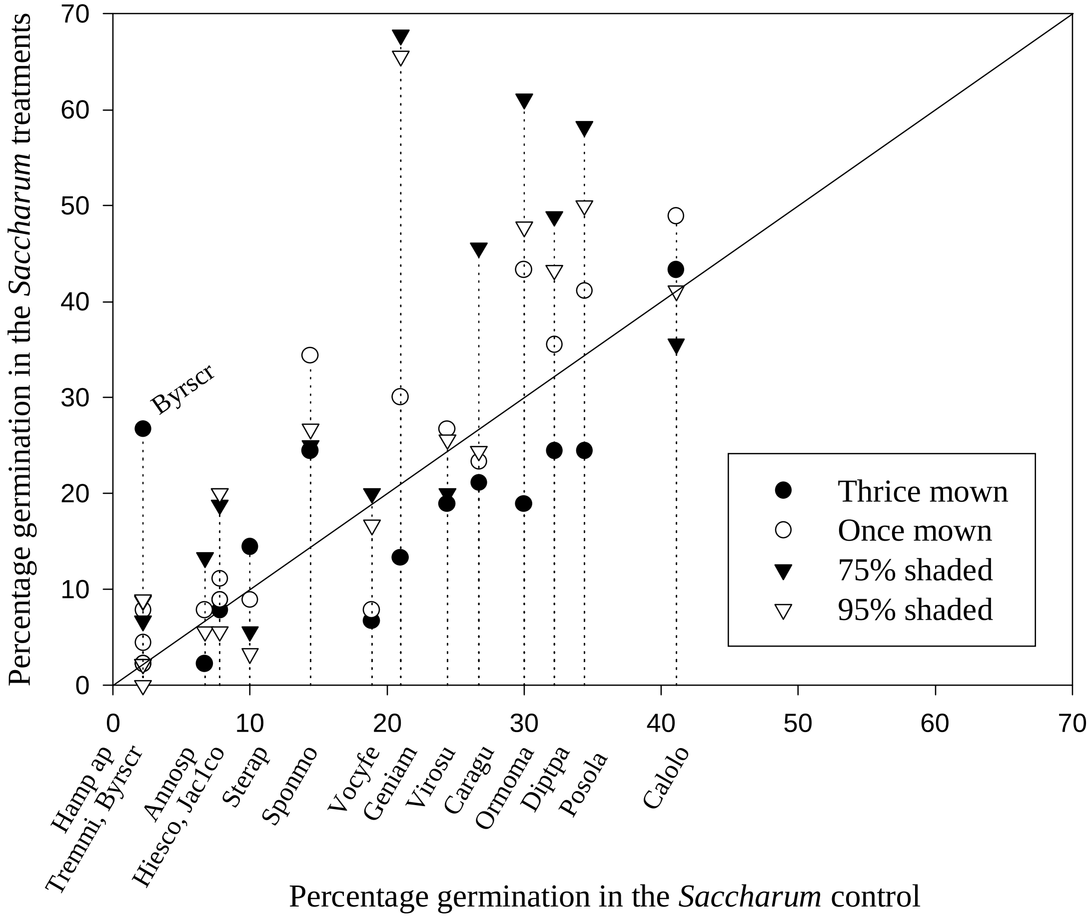
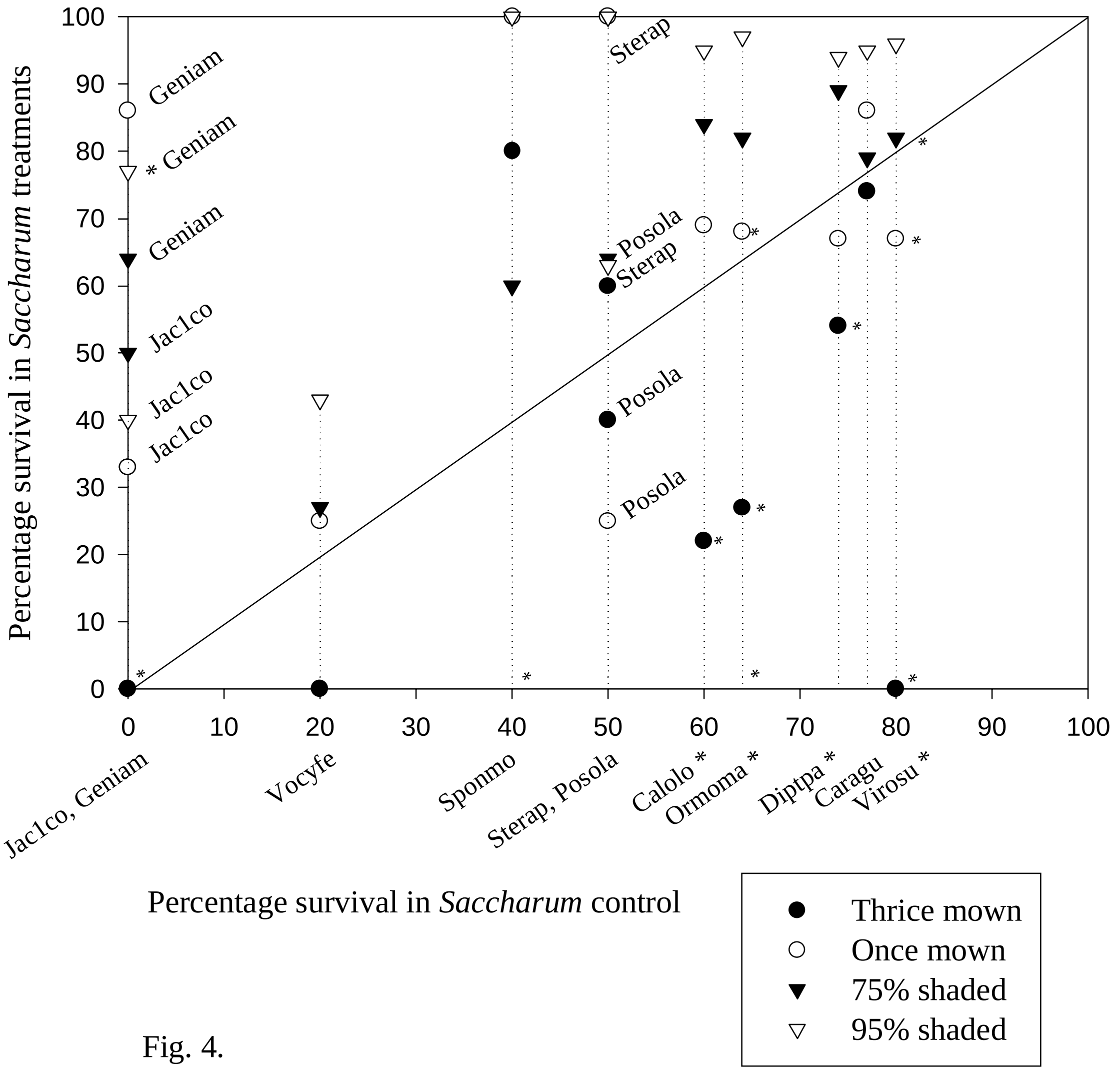

1.00
0.50
0.00
-0.50
-1.00
-1.00
-0.50
0.00
0.50
1.00
RDA Axis 2
RDA Axis 1
Thrice mown and 95% shaded^a
Once mown^b
Thrice mown^b
Control^b
Thrice mown and 75% shaded^a
Sponmo
Hampap
Heisco
Geniam
Diptpa
Ormoma
Posola
Virosu
Calolo
Byrscr
Sterap
Annosp
Vocyfe
Caragu
Jac1co
Tremmi
Seed Size:
● = very-small-seeded (0 - 0.1 g)
■ = small-seeded (0.1 - 1 g)
▲ = large-seeded (1 - 10 g)
▼ = very-large-seeded (> 10g)
Light index:
white = pioneer / large gap (> 0.75)
grey = small gap (0.75 to –0.75)
black = light dependence (< –0.75)

Fig. 2.



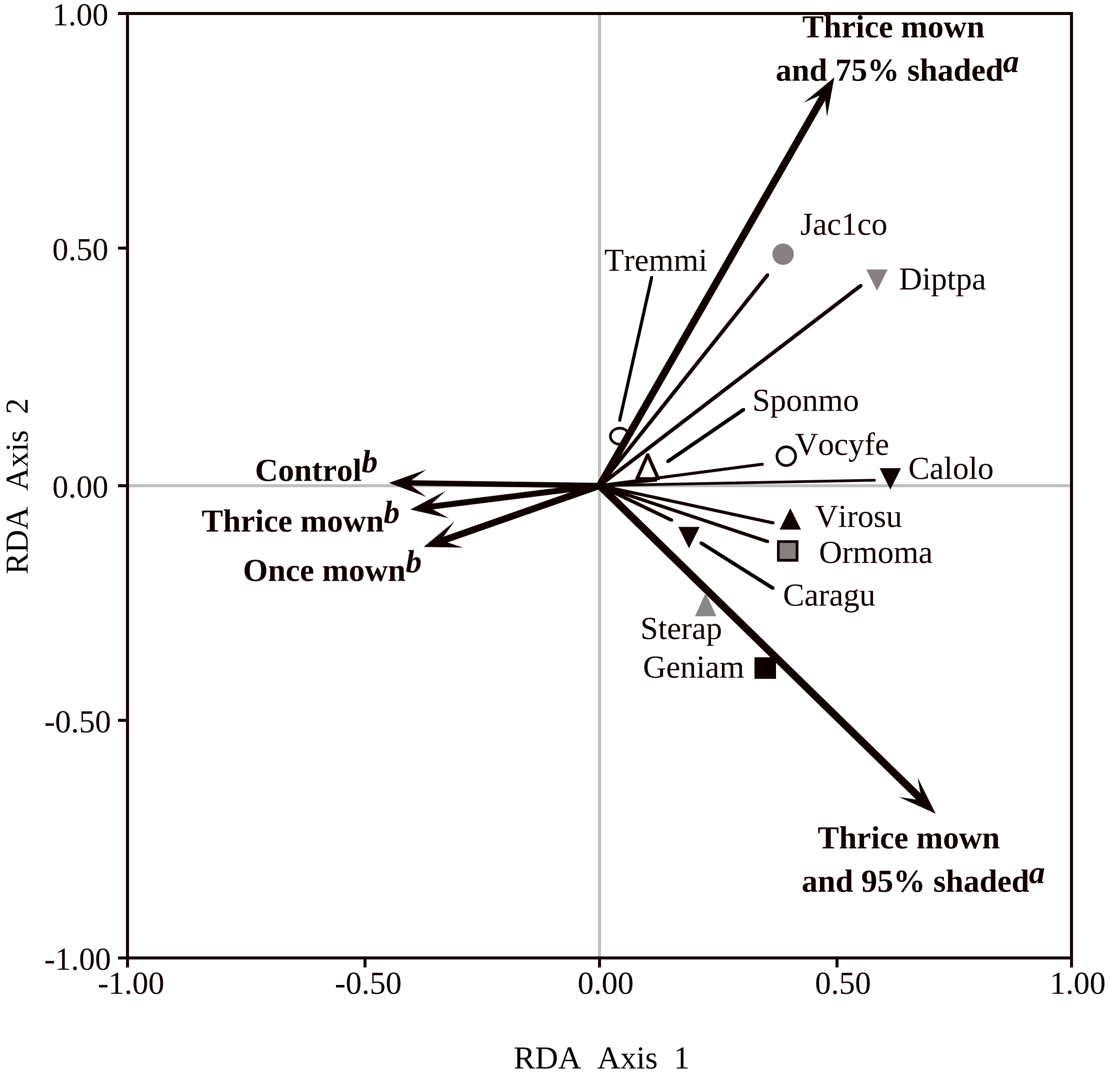
Percentage germination in the *Saccharum* treatments
Percentage germination in the *Saccharum* control
0
10
20
30
40
50
60
70
Byrscr
Hamp ap
Tremmi, Byrscr
Annosp
Hiesco, Jac1co
Sterap
Sponmo
Vocyfe
Geniam
Virosu
Caragu
Ormoma
Diptpa
Posola
Calolo
● Thrice mown
○ Once mown
▼ 75% shaded
▽ 95% shaded

Fig. 3.



Percentage survival in *Saccharum* treatments
Percentage survival in *Saccharum* control
0
10
20
30
40
50
60
70
80
90
100
Geniam
* Geniam
Geniam
Jac1co
Jac1co
Jac1co
Sterap
Posola
Sterap
Posola
Posola
*
Jac1co, Geniam
Vocyfe
Sponmo
Sterap, Posola
Calolo *
Ormoma *
Diptpa *
Caragu
Virosu *
● Thrice mown
○ Once mown
▼ 75% shaded
▽ 95% shaded

Fig. 4.



1.00
0.50
0.00
-0.50
-1.00
-1.00
-0.50
0.00
0.50
1.00
RDA Axis 2
RDA Axis 1
Thrice mown and 75% shaded^a
Thrice mown and 95% shaded^a
Control^b
Thrice mown^b
Once mown^b
Jac1co
Tremmi
Diptpa
Sponmo
Vocyfe
Calolo
Virosu
Ormoma
Caragu
Sterap
Geniam

Fig. 5.

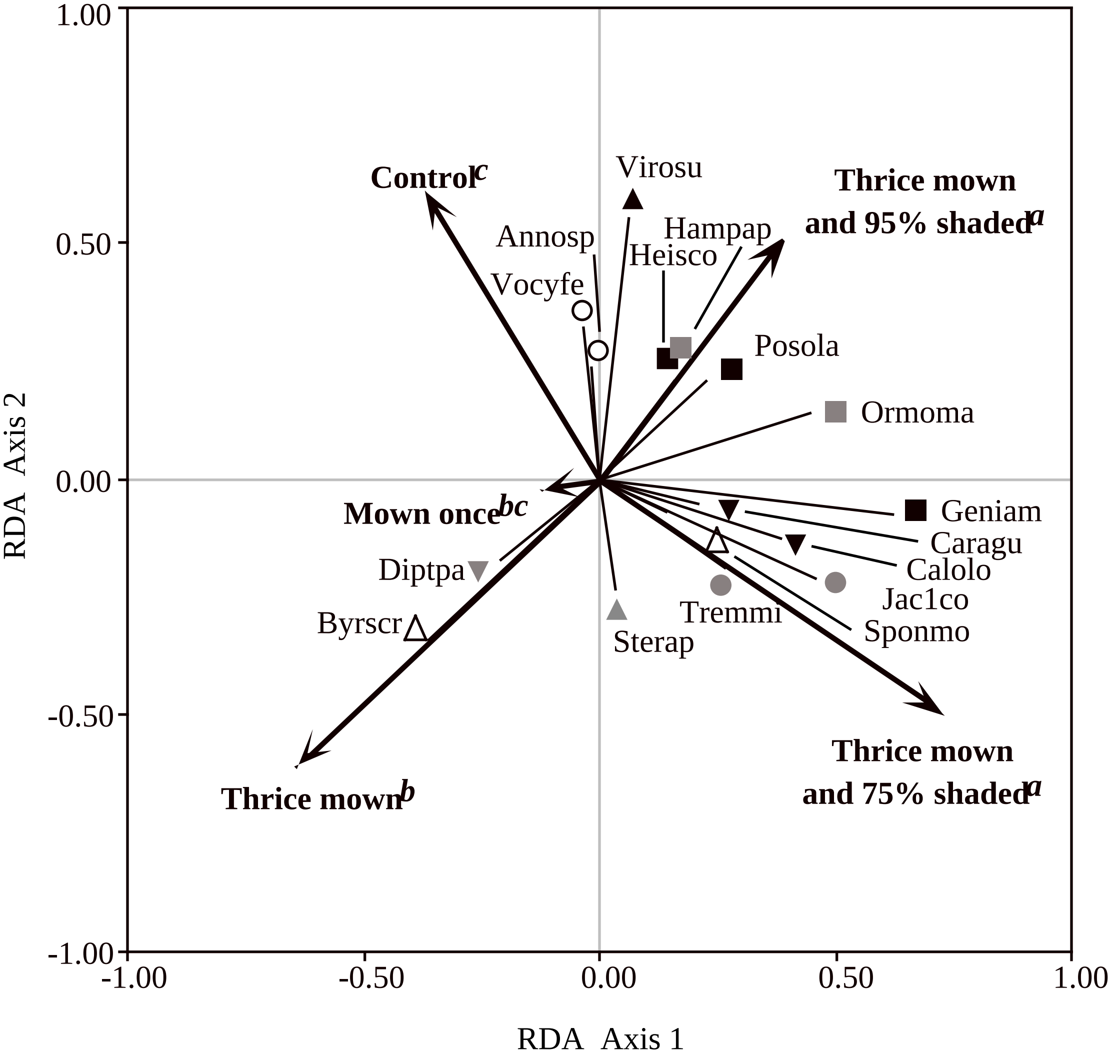

1.00
0.50
0.00
-0.50
-1.00
-1.00
-0.50
0.00
0.50
1.00
RDA Axis 2
RDA Axis 1
Control c
Virosu
Thrice mown and 95% shaded a
Annosp
Hampap
Heisco
Vocyfe
Posola
Ormoma
Mown once bc
Geniam
Caragu
Diptpa
Calolo
Jac1co
Byrscr
Tremmi
Sponmo
Sterap
Thrice mown and 75% shaded a
Thrice mown b

Fig. 6.

APPENDIX 1. Summary of analysis of variance (ANOVA) with repeated measures on % germination, % abundance, % survival, height (cm) and relative height growth x 10^{-3} day^{-1} (RHT). The analysis followed a repeated measures, split-plot design. Sources of variation included distance from the forest as the main plot factor (distance), shading and mowing treatments of the *Saccharum* as the sub-plot factor (treatment), and their interactions. Site was included as a blocking factor. * P < 0.05, ** P < 0.01, ***P < 0.005

	Germination†		Abundance†		Survival†		Height‡		RHT‡	
Source	df	F	df	F	df	F	df	F	df	F
Between subjects										
Distance	2	0.52	2	3.39	2	1.11	2	3.52	2	4.77
Site x distance	4	Main plot error								
Treatment	4	11.68***	4	13.04***	4	2.79*	4	3.22**	4	4.86**
Treatment x distance	8	0.69	8	0.45	8	0.43	8	0.22	8	0.58
Site x treatment + Site x treatment x distance	24	Sub-plot error								

Within subjects										
Time	2	36.31***	3	80.73***	2	1.71	2	5.68**	2	0.86
Time x distance	4	0.59	6	1.01	4	0.15	4	2.17	4	0.13
Time x site x distance		Main plot error								
Time x treatment	8	1.84	12	2.82**	8	1.09	8	1.08	8	0.26
Time x treatment x distance	16	0.92	24	0.80	16	0.74	16	0.36	16	1.08
Time x site x treatment + Time x site x treatment x distance		Sub-plot error								

Notes:

† n = 45 subjects (i.e. 45 unburned subplots); ‡ n = 371 subjects (i.e. 371 seedlings were present over all 3 time periods in the 45 unburned subplots)

Appendix 1 continued

APPENDIX 2. Summary of RDA in a MANCOVA-like design on matrices of germination per species per sub-plot per time period (Germination) or relative growth rates for height x 10^{-3} day^{-1} per species per subplot per time period (RHT). Sources of variation included distance from the forest (distance), shading and mowing treatments of the *Saccharum* (treatment), time and their interactions. Site and the interaction of site with all main factors and interactions were utilized as covariables. * P < 0.05, ** P < 0.01, ***P < 0.005 (determined using permutation testing).

	Germination		RHT	
Source	df	F	df	F
Site	2		2	
Distance	2	1.03	2	1.41
Treatment	4	2.89**	4	4.67***
Treatment x distance	8	0.70	8	1.25
Time	3	31.51**	1	12.08**
Time x distance	6	1.01	2	2.46*
Time x treatment	12	1.81**	4	2.85***
Time x treatment x distance	24	0.72	8	1.36