

Competitive ability and seedling establishment of *Cinnamomum verum* and *Phoenicophorium borsigianum*

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Abstract: In Seychelles the endemic palm *Phoenicophorium borsigianum* and the aggressively invasive alien *Cinnamomum verum* are competitors. The extent to which demographic variables are determinants of competitive ability in these species was investigated. The effects on competition of morphological responses to light intensity were investigated with consideration of the extent to which native plants can establish, regenerate and potentially outcompete *Cinnamomum* in important biodiversity sites. Light intensity in terms of diffuse site factors was established from computerized image analysis of hemispherical photographs. A new plant growth analysis function, leaf area/height index (ALHI), has been introduced and a principal components analysis was carried out to evaluate seedling performance. Competition between *Cinnamomum* and *Phoenicophorium* was greatly influenced by the amount of available photosynthetically active radiation. *Phoenicophorium* and probably other native palms act as a filter affecting the distribution and abundance of establishing *Cinnamomum* seedlings. Unlike *Phoenicophorium*, *Cinnamomum* could establish and regenerate only at relatively high light levels.

Keywords: demography; diffuse site factor; plant growth analysis; Seychelles

Introduction

Earlier studies on the invasion of alien plants in the Seychelles showed that *Cinnamomum verum* and *Phoenicophorium borsigianum* (hereafter *Cinnamomum* and *Phoenicophorium*) shows highest prominence values on the islands of Mahé and Silhouette (Fleischmann 1997). The endemic palm *Phoenicophorium* showed an outstanding potential to maintain and establish itself in secondary forests and in areas suffering from serious forest destruction, while *Cinnamomum* proved to be the most aggressive alien invader in Seychelles forests. This remarkably dynamic performance makes these species competitors in a series of habitats in the Seychelles. A major objective of this study was to investigate the extent to which growth in leaf area and growth in height, together with mortality and recruitment, contribute to the competitive ability of *Phoenicophorium* and *Cinnamomum*.

Phoenicophorium borsigianum Wendl. (Oncosperma alliance) is a palm endemic to the Seychelles, reaching a maximum height of 15 m. It is a hillside palm and, besides *Cinnamomum*, is probably the most prominent plant in the study area (Fleischmann 1997).

Cinnamomum verum Presl. (Lauraceae) is a cultivated and invasive shrub or tree up to 17 m tall with aromatic bark and leaves.

One approach to explain the competitive relations between the two species was to measure growth characteristics such as the relative increase in height and the relative increase in leaf area. A comparison of seedling performance of *Phoenicophorium* and *Cinnamomum* directly under different light levels was envisaged. To achieve this, a new plant growth analysis function, the so-called leaf area/height index (ALHI, see below), has been introduced and a principal component analysis (PCA) was carried out to investigate competitive ability. Furthermore, it was investigated whether or not competitive ability can

change with light intensity as a result of different morphological responses. Drawing attention to pragmatic questions related to forest management in the Seychelles, it was asked what extent native plants like *Phoenicophorium* can establish, regenerate and potentially outcompete *Cinnamomum* in important biodiversity sites on Mahé island. In view of the increasing invasion by the alien *Cinnamomum* into relatively un-disturbed forest habitats, this question becomes increasingly relevant to community conservation planning in the present day Seychelles.

Methods

Study sites

The study area comprises four sites in intermediate forests and lower parts of moist rain forest on Mahé island, Seychelles, where the topography is relatively level. The study sites were as follows:

'La Réserve': Plateau on ascent towards summit of Montagne Brulée, a somewhat flat area in mature *Northea* - *Deckenia* woods at 430 m altitude.

'Swietenia forest': Slightly sloping area below 'La Réserve' at 405 m altitude with rather open woods dominated by the recently introduced *Swietenia macrophylla*.

'Obelix': Ridge in Congo Rouge, West of Morne Seychellois. Moderately sloping area at 770 m altitude in mature *Northea hornei* - *Roscheria melanochaeta* forest.

'Jumeau': Open Plateau at 200 m altitude East of Montagne Brulée with a vegetation in post-fire succession. Last fire, December 1990.

With the exception of sites 'Jumeau' and 'Swietenia forest', which have been somewhat disturbed by human activity in the past, these forest sites can be described as mature. 'La Réserve' and 'Obelix' have probably seen very little human disturbance since the Seychelles were discovered 250 years ago.

Calculation of leaf area

Annual leaf area increments were calculated separately for *Phoenicophorium* and *Cinnamomum* seedlings and saplings <200 cm tall as in Fleischmann (1997a). Juveniles in this size category are hereafter called seedlings. The analysis of leaf area was performed in three different light climates: high canopy sites (diffuse site factors <mean, i.e. <29.9% DifSF [see below]); low canopy sites (DifSF=29.9–44.5%) and gaps (DifSF=98.7%). DifSF is the fraction of incident diffuse radiation transmitted by holes in the canopy; i.e. the canopy openness (Turner 1990). The light climate of the study sites and the study area are described in Fleischmann 1997a (PART-II and PART-I respectively).

Correlation between leaf area and plant height

Regression lines of average leaf area (AL) on plant height (H) were fitted by the least square method. For *Cinnamomum* a linear regression was found to fit adequately (Fig. 1a) while *Phoenicophorium* showed its best fit with an exponential regression (Fig. 1b).

Knowing that within the selected range of seedling sizes, the regression between AL

and H was basically linear in any particular light regime, it is possible to estimate the average leaf area of a seedling by its height. Increments of average leaf areas were calculated over the whole range of seedling sizes by regressing the height of a seedling at the beginning and at the end of the intercensus period (i.e. 1993 – 1994) against the corresponding average leaf area in Fig. 1. The regression functions (in terms of curves of best fit) are shown in Figures 1a and 1b.

Growth-analysis calculations

It is well known that increased production of leaf area may compensate for a lower net assimilation in low-light conditions, so that relative growth rates in height remain constant (Blackman & Wilson 1954; Hughes 1966). Moreover, plant growth rates are also affected by self-shading and by plant size. Because of this, both the increments in total leaf area per plant and the increase in height were measured simultaneously for an estimation of the above-ground growth performance of seedlings. The analysis of other growth parameters like the rate of branch production or the increase in girth were omitted for practical reasons. Furthermore, Turner (1990) showed that for seedlings and saplings <200 cm the increase in girth could not be related to different levels of PAR, and Oberbauer *et al.* (1988) reasonably inferred that height growth was more important than stem growth for saplings aspiring for canopy.

Growth analysis was used here as a tool to obtain insight into the functioning of a plant, and increments in plant height and leaf area were assumed to be key factors. Following the procedure recommended by Lambers *et al.* (1992) the growth performance in terms of the leaf area/height index (ALHI, see below) was factorized into two components, the relative growth rate of leaf area (RGRAL) and the relative growth rate of height (RGRH). The height (H) of a seedling is the distance between the ground and its terminal leader. The height and total leaf area of 159 *Phoenicophorium* and *Cinnamomum* seedlings were transformed to logarithms to stabilize the variances. The mathematical procedure was as follows:

$$ALHI = \frac{\ln(H_t) - \ln(H_0)}{t} + \frac{\ln(AL_t) - \ln(AL_0)}{t}$$

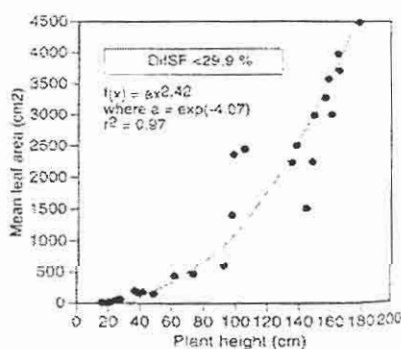
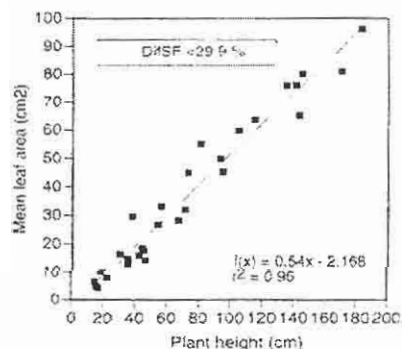
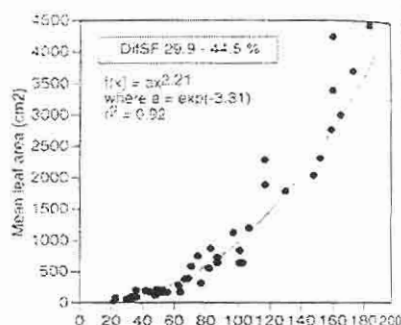
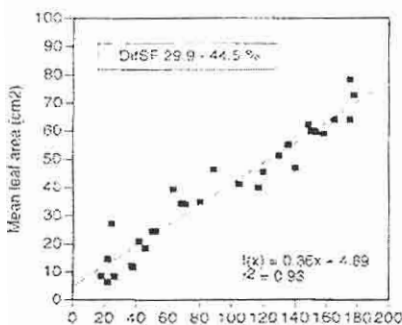
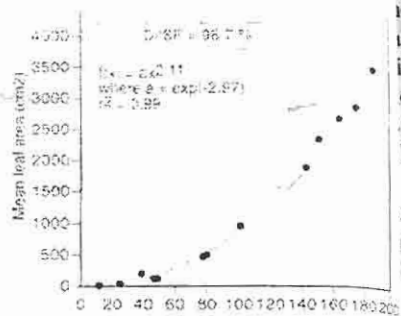
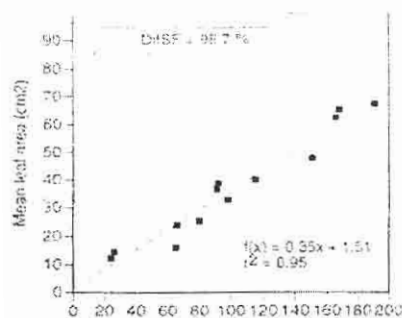
where ALHI is the leaf area/height index and H the height of a seedling, AL is the leaf area and \ln the natural logarithm, measured at time t and at time 0. The statistics were calculated with SYSTAT (Version 5.2.1).

Leaf thickness

Leaf thickness of *Cinnamomum* and *Phoenicophorium* seedlings was measured with microcalipers. The variation in leaf thickness with light levels and seedling height was investigated.

Principal component analysis (PCA)

For the overall seedling performance of *Cinnamomum* and *Phoenicophorium* a PCA was carried out using the following parameters: (a) colonization, (b) mortality (resp. survival), (c) growth in height and (d) growth in leaf area. PCA has been widely used to define plant functional types (Golluscio & Sala 1993; Franklin *et al.* 1995). Based on the paradigm



a) *Cinnamomum verum*

b) *Phenicoophorium borsigianum*

Fig. 1. Regression functions of average leaf area against plant height in three different environments. The regression functions give an estimation of average leaf area from the height of *Cinnamomum* and *Phenicoophorium* seedlings <200 cm tall.

competitive ability of tree species in tropical forests (Whitmore 1993) a high correlation among the variables, with the first principal component reflecting competitive performance, is assumed. It was evaluated whether the demographic variables - as condensed by principal components - predicted population change and under which light climate the endemic *Phoenicophorium* was suitable to replace *Cinnamomum*. Correlations were tested using Spearman's rank test and associations between continuous and nominal variables (classes of DifSF) with the Mann-Whitney U-test.

Results

Growth and seedling establishment of *Phoenicophorium* and *Cinnamomum*

Growth

Mean leaf areas of *Cinnamomum* and *Phoenicophorium* seedlings were significantly larger beneath a closed canopy than in low canopy. For both species a negative correlation between mean leaf area of seedlings and DifSF was found (*Cinnamomum* $r_s=0.371$; $p<0.005$; *Phoenicophorium* $r_s=0.547$; $p<0.001$). This general trend was compensated in *Cinnamomum* seedlings by a significantly higher number of leaves per plant in low canopy sites ($F=19.772$; $p<0.001$). *Cinnamomum* seedlings had 3-30 leaves per plant while *Phoenicophorium* had only 1-6 leaves.

Beneath closed canopies *Phoenicophorium* showed a higher efficiency of leaf display in terms of leaf area growth rates (RGRAL) and leaf area/height indices (ALHI) (Table 1). However, under higher light levels the relative height growth rate (RGRH) of *Cinnamomum* significantly exceeded that of *Phoenicophorium*. Over the range of light conditions *Phoenicophorium* showed better growth performance in ALHI and significantly better performance in RGRAL than *Cinnamomum* (Fig. 2).

In areas with lower than average light levels the relationship between annual leaf area increments and seedling height differed remarkably for the two species; *Phoenicophorium* showed significantly higher increments for larger plant sizes than *Cinnamomum*. The expected positive correlation between plant height and the corresponding annual increment in leaf area was not found for *Cinnamomum* seedlings in sites with DifSF $<7.5\%$ (Fig. 2b).

Leaf thickness

In areas of both high and low cover, the correlation between the height of *Cinnamomum* seedlings and the thickness of leaves was significant ($r_s=0.748$; $N=19$; $p<0.005$). Increase in leaf thickness with increasing plant size was more pronounced in the more open sites. *Cinnamomum* leaves were generally thicker in low canopy, although not significantly (Mann-Whitney U test: $U=197.5$, $p=0.56$) sites. The thickness of *Phoenicophorium* leaves was neither correlated with the levels of light nor with the height of seedlings, except in leaves of less than 30 cm length, in which the leaf blades were slightly thinner, independent of light conditions.

Mortality

The mortality of *Cinnamomum* was strongly negatively correlated with DifSF ($r_s=-0.478$, $N=27$, $p<0.01$) while *Phoenicophorium* showed no correlation (Spearman: $r_s=-0.170$, $N=19$, $p>0.05$). For *Cinnamomum* the mortality was significantly higher in areas

light intensity (Mann-Whitney: $U=148$, $p=0.003$); this was not true for *Phoenicophorium* (Mann-Whitney: $U=48.5$, $p=0.667$). In high canopy sites *Phoenicophorium* did survive better, though, in comparison with *Cinnamomum*, no significant difference was found between the two species (ANOVA: $F=3.416$; $p=0.076$).

Recruitment

In areas with below average light *Cinnamomum* recruited significantly better than *Phoenicophorium* (Mann-Whitney: $U=292.0$, $p=0.001$). Unexpectedly, recruitment of the other species was particularly strong in low canopy sites with high levels of PAR (Table 2).

Competitive ability of *Phoenicophorium* and *Cinnamomum*

As predicted, significant correlations between the demographic variables and diffusive site factors were found. For *Cinnamomum* there were significant positive correlations with growth (for both RGRAL and RGRH) and survival. Of all demographic variables, only the colonizing index of *Cinnamomum* was not significantly correlated with the level of light. This means that a species like *Cinnamomum* with generally high colonizing indices tends to have higher competitive ability with increasing levels of PAR.

Table 1. ALHI, RGRAL and RGRH of seedlings in all plots and in plots of <mean DifSF and >mean DifSF. Asterisks represent differences between the two subgroups; * $p<0.05$, ** $p<0.005$, † $p=0.05$; n.s.=not significant; Cinn = *Cinnamomum*, P = *Phoenicophorium*.

DifSF	ALHI (mean)			GRAL (mean)			GRH (mean)		
	Cinn.	P.	F (species)	Cinn.	P.	F (species)	Cinn.	P.	F (species)
<29.9	0.33	0.58	3.68 †	0.2	0.43	5.94*	0.13	0.15	0.35 n.s.
>29.9	0.44	0.5	0.17 n.s.	0.21	0.38	2.17 n.s.	0.23	0.12	4.84 *
Full range	0.36	0.55	3.5 n.s.	0.2	0.41	8.08 **	0.16	0.14	0.39 n.s.
Effect of DifSF for same species F	1.65 n.s.		0.12 n.s.	0.04 n.s.		0.007 n.s.	10.08 ** 0.29 n.s.		

Table 2. Growth (ALHI), mortality (MI) and recruitment (CI) of *Cinnamomum* and *Phoenicophorium* seedlings in all plots and in plots of <mean DifSF and >mean DifSF.

DifSF	<i>Cinnamomum</i>			<i>Phoenicophorium</i>		
	ALHI	MI	CI	ALHI	MI	CI
<15	0.31	30.79	28.07	0.56	16.67	9.66
15-29.9	0.35	24.4	24.47	0.60	10	5.47
30-44.9	0.56	4.76	11.16	0.50	6.67	4.54
98.7	0.35	8.33	56.95	0.50	5.56	5.09
<mean DifSF	0.33	27.99	26.37	0.58	13.64	7.76
>mean DifSF	0.44	6.06	25.25	0.50	6.25	4.71
Range of DifSF	0.36	19.06	25.91	0.55	10.53	6.47

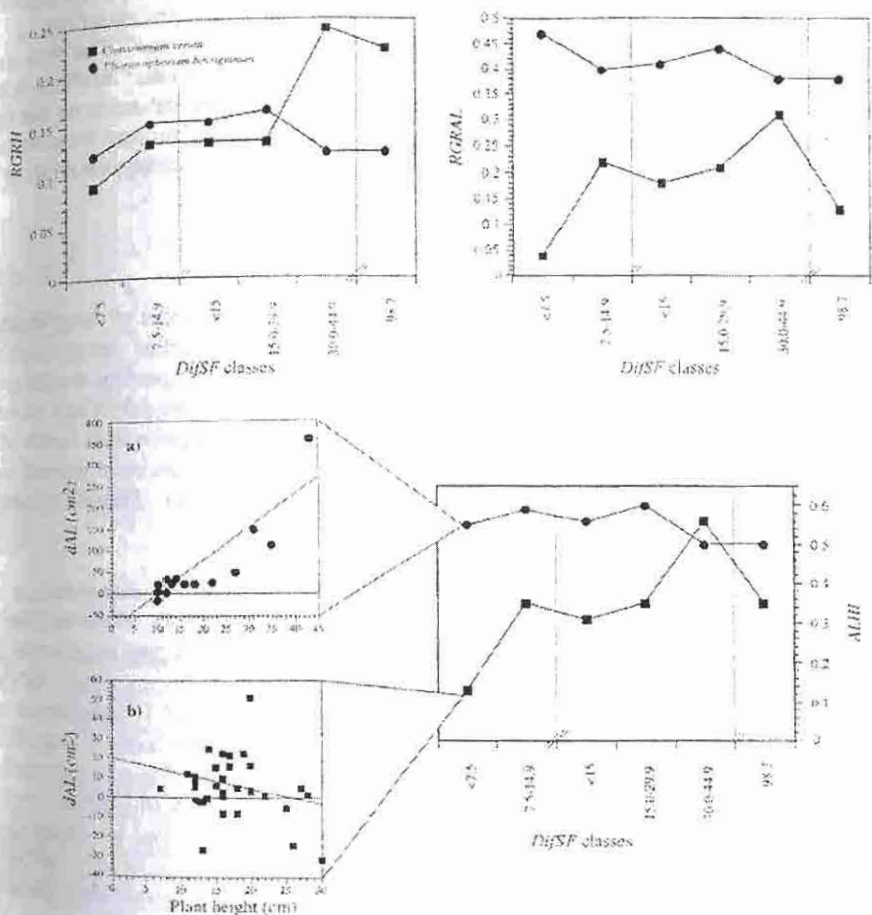


Fig. 2. Graphs of leaf area/height index (ALHI), relative growth rates of height (RGRH) and leaf area (RGRAL) against classes of DifSF for *Cinnamomum* and *Phoenicophorium* seedlings. Figs. 2a and 2b demonstrate a remarkable difference in leaf growth between the two species in very dark areas; i.e. *Phoenicophorium* showed significantly better growth performance over the range of seedling sizes. dAL, annualized increase of leaf area.

For *Phoenicophorium* the colonizing index was significantly and positively associated with mortality over the range of available PAR. In terms of all demographic variables investigated, seedling performance of *Phoenicophorium* was significantly reduced in areas of above average light. This means that, unlike *Cinnamomum*, the endemic *Phoenicophorium* tends to have higher competitive ability in shadier forest sites (Fig. 3).

The principal components analysis reflected these correlations. The first axis accounted for 64.5% of all variation with the following correlations: $RGRAL = 0.70$, $survival = 0.55$ and $recruitment = -0.54$. Thus, a species' score on the axis is a composite of the four correlated demographic variables, and reflects the predicted axis of competitive ability. High scores indicate a strong tendency to outcompete rivals (Fig. 4).

Discussion

Recruitment of *Cinnamomum* vs. *Phoenicophorium*

Swaine & Whitmore (1988) define pioneers by their requirement of direct sunlight for germination. In Seychelles *Cinnamomum* is often found in disturbed forest areas and seedlings of this species established themselves significantly better in openings than in areas with a continuous forest canopy. *Cinnamomum* can therefore be distinguished as a pioneer. On the other hand, because of its high colonizing index even in areas with light levels of -29.9% and its potential to establish under such light levels, *Cinnamomum* proved to be relatively shade tolerant as well. However, compared with *Phoenicophorium* *Cinnamomum* could not compete in the shadiest areas $<7.5\%$ DifSF.

Growth of *Cinnamomum* vs. *Phoenicophorium*

ALHI gave information about the growth dynamics of *Phoenicophorium* and *Cinnamomum* seedlings and their response to different levels of light. *Phoenicophorium* responded significantly better in terms of RGRAL and ALHI to low gap light levels than *Cinnamomum*. None of the growth parameters showed any further response to increasing sunlight with light levels of 98.7% DifSF (Fig. 2). Seedlings of *Cinnamomum* were capable of responding to more open environments with much higher indices of both, RGRAL and ALHI than to closed forest areas. This supports the hypothesis that establishment and invasion of *Cinnamomum* is much facilitated by gap formation. Seeds of *Cinnamomum* germinate rapidly and logging clearings or treefall gaps are often filled by single species stands of this plant. This observation suggests that nearby trees producing seeds at the time when a gap is formed have a competitive advantage over seedlings germinating from distant banks.

On the other hand, the ability of *Phoenicophorium* seedlings to increase leaf area indices in low light levels without proportional increases in plant height suggests that they were capable of increasing the fraction of radiation intercepted by leaves without a significant increase in the metabolic costs of producing and maintaining stems and branches to support the leaves. It seems likely that this variation in leaf display was an important component of the surprisingly high ALHI for *Phoenicophorium* in high canopy sites with DifSF $<15.0\%$. The comparatively modest growth response to low light combined with a significantly higher mortality rate of *Cinnamomum* shows that in forest areas with DifSF $<15.0\%$ the endemic *Phoenicophorium* is able to outcompete *Cinnamomum*, one of the most aggressive alien invaders in Seychelles.

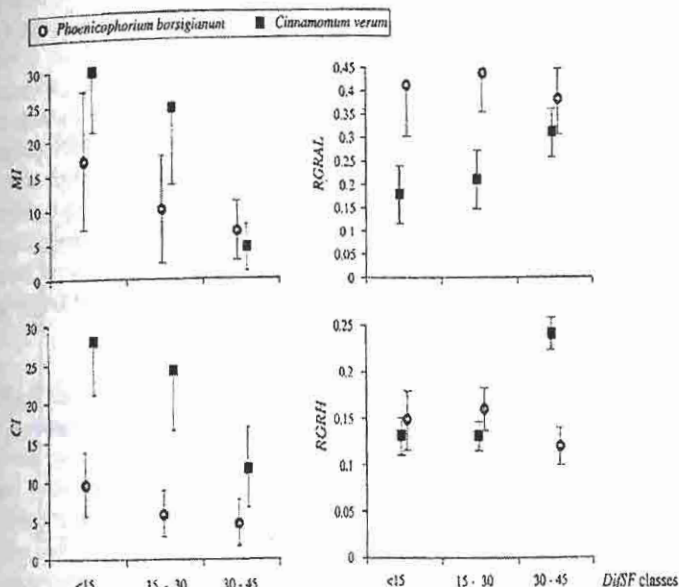


Fig. 3. The relationship between classes of DifSF and mortality (MI), colonization (CI), relative growth rate of leaf area (RGRAL) and relative growth rate of height (RGRH) for *Cinnamomum* and *Phoenicophorium* seedlings (\pm SE).

The slower leaf area development of *Cinnamomum* in high cover areas with available PAR of <29.9 % DifSF reduced its capacity to capture light, which then reduced its RGRH compared to *Phoenicophorium*. This study shows that competition between *Phoenicophorium* and *Cinnamomum* was probably greatly influenced by the amount of available PAR.

Phoenicophorium is able to germinate under a closed canopy, although some opening is necessary for growth to reproductive sizes. The seeds of *Phoenicophorium* are small and animal dispersed. Seedlings produce relatively large leaves in a short time and are able to persist for long periods and recover repeatedly from insect damage.

Canopy closure seems to promote seedling germination of *Phoenicophorium* through changes in the environmental conditions in the forest floor, which might be related to decreasing radiation and water evaporation. Greenhouse experiments (Espalta *et al.* 1995) have shown that reduced light levels and an associated increase in soil moisture content can have a positive effect on seedling germination and seedling growth. This is obviously true for *Phoenicophorium* for which seedling growth did not necessarily increase with a high level of PAR.

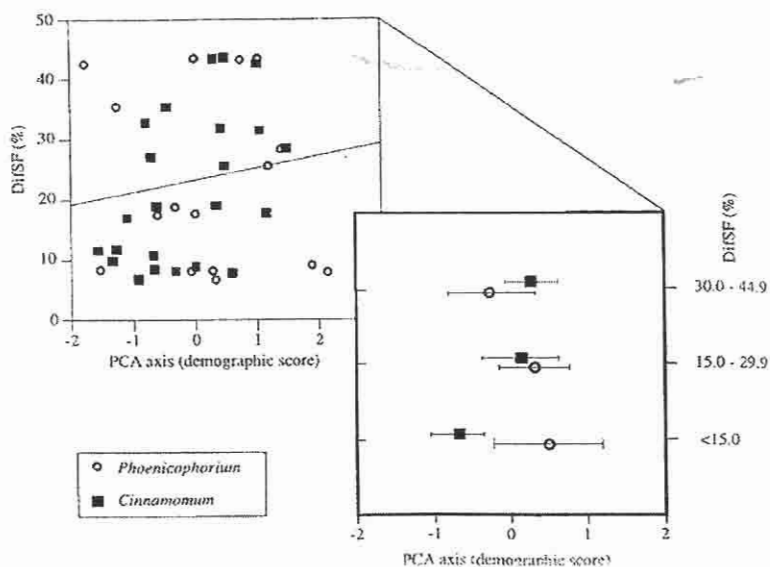


Fig. 4. The relationship between DifSF classes and the demographic score (first PCA axis). Each point represents the situation in a single sample plot. A condensed form of the values is given on the right.

Conservation

Phoenixophorium can be considered a high canopy specialist. Its shade tolerance and capacity to grow even at very low light levels make this palm particularly successful in competing with *Cinnamomum* and probably other invaders like *Adenanthera pavonina*, *Tabebuia pallida*, *Hevea brasiliensis* etc. in shaded forest areas (i.e. DifSF < 15%). In terms of community conservation planning in Seychelles National Parks, it seems advisable to use these promising results to reduce the invasion by *Cinnamomum* in endangered biodiversity sites.

For *Cinnamomum* a DifSF below 7.5% was strongly limiting. Once the canopy was closed and radiation to the forest floor reduced to this low level, growth and further survival of *Cinnamomum* seedlings were greatly reduced. This study suggests that *Cinnamomum* as well as *Phoenixophorium* seedlings may indeed demonstrate different optima along the understory cover gradient. These findings are consistent with those of Fenner (1978) and Denslow (1980) who gave evidence that some shade-tolerant tropical tree species rely on optimal light intensities for seedling growth and seedling establishment within the understory.

environment, and that these optima differ among species.

The fact that RGRH of both species correlated significantly with RGRAL suggests that the efficiency with which light is absorbed by a leaf depends largely on the leaf area and hence on the content of chlorophyll per unit leaf area. The question of whether the two species differ in other photosynthetic characteristics as well could not be answered in this study. Simulations for understory palms (Chazdon 1986) show that when most of the total daily PAR is diffuse radiation, which is the case in most of this study area, the relation between total daily PAR and total daily net assimilation is linear.

The data from this study suggest that *Phoenicophorium* is an important competitor with the seedlings of *Cinnamomum* and probably other invasive species and may, through its effect on the composition of the seedling pool, ultimately influence the structure and dynamics of the forest. In some of the study sites with low light levels (e.g. La Réserve) the understory is often dominated by *Phoenicophorium* treelets.

Conclusion

A comparison of *Cinnamomum* and *Phoenicophorium* showed that the former can be regarded as pioneer while *Phoenicophorium* is a high canopy species. This study demonstrated that the two species represent contrasting functional groups in the sense that *Cinnamomum* was fast-growing and light demanding and survived significantly better in open areas, whereas *Phoenicophorium* showed opposite trends. In this respect a simple paradigm - the pioneer/shade-tolerant dichotomy (Whitmore 1993) worked quite well to describe the demography of these two species. However, this simple contrast had two anomalies: First, the decreasing colonizing index with increasing levels of PAR for both species is not consistent with the pioneer/shade tolerant dichotomy. It may be that the propagation of *Cinnamomum* and *Phoenicophorium* seeds, which depends largely on birds or gravity, is enhanced in habitats near parent-trees so that gaps do not enhance recruitment if they are far from seed sources. Second, *Phoenicophorium* showed not only shade tolerance but also an outstanding plasticity in establishing itself in a broad range of light levels. This plant was even found in exposed areas on inselbergs and on denuded slopes. This study shows that a model describing forest dynamics could be based on demographic parameters.

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