VI. DISCUSSION
DISCUSSION

I. Comparison of series

Species and life-form turnover

The 2nd year, 4th year, 10th year series in spontaneous and 2nd year, and 6th year, series in directed successions and spontaneous succession can be considered to be early seral stages when an increase in diversity followed by a decline is expected (Tramer 1975; McCook 1994; Singh et al 2006). The 12th year series in directed successions & 50th year series in spontaneous succession where the secondary tree species increase and appear in greater abundance (12 & 16 tree species) can be considered as the beginning of the middle seral stages of secondary succession. The percentage of herbs seen in the spontaneous succession is 51%, and shrubs and undershrubs was 26% and trees & lianas make up 23%, while the percentage of herbs seen in the directed succession is 40%, and shrubs and undershrubs was 20%, and trees & climbers make up 40%. The higher species richness seen due to protection is similar to other studies, where species richness increased due to protection from grazing in Venezuelan savannah (Jose – Frairnas 1983), Sahel, Africa (Hernaux 1998) and abandoned Amazonian pastures (Uhl et al.1988). The woody species are in excess of that recorded earlier (10%) for the area by (Blasco & Legris 1973).

A progressively decrease of herbaceous diversity, and increase in woody species diversity reflected by Hill’s H0 number, Simpson’s (1/D) and Shannon’s H’ indices (Table 1 and Fig. 1) through the series was discerned. The percentage of woody species is also higher
in directed seres than in spontaneous seres, indicating a faster rate of succession. There was more diversity in protected areas, even in terms of number of families and genera reflecting the survival of species that are sensitive to grazing (Heinnaux 1998) (Table 2a & b).

Secondary succession is better explained by turnover of life-forms (Pickett et al. 2001), and in this succession, woody species both shrubs and pioneer trees were seen in the 2nd year, but they dominate only in later seres. In protected areas, pioneer shrubs (Canthium parviflorum) and trees (Azadirachta indica and Morinda pubescens) are seen in the 2nd year, but shrubs become predominant only in the 6th year seres, and trees in the 12th seres, where secondary species & primary forest species dominate. In the open areas, three shrub species appear in the 2nd year seres, and except for the common secondary /pioneer tree species like Azadirachta indica, Prosopis juliflora, Borassus flabillifer and a liana Zizyphus oenophia, whose saplings were recorded in the 2nd and 4th year seres, most of the secondary tree species are able to establish themselves only in the end of early and beginning of middle successional stages – 50 year seres. In another tropical dry forest (Aide et al. 1996) found shrubs and trees dominating after 20-30 years.

Some of the herbs that grow and persist in both pathways were similar like Spermacoce spp., Hedyotis puberula and Evolvulus alsinoides. There are more leguminous species (Desmodium trifolia & Teramnus tridentate) abundant in the first two seres that are protected, but not in the open area. Though Perotis indica, Aristida setacea and Heteropogon contortus are common to both seral types, they lose their dominance in the
protected sites to shrubs and trees by the 12th year, but persist till 50 years in open areas. *Sehima nervosum* the most abundant species in the 12th year protected sites is rare in open areas. Many species of grass like *Bothriochloa pertusa, Chrysopogon fulvus, Sehima nervosum, Heteropogon contortus* and *Dactyloctenium aegyptium* species typically found in disturbed grasslands (Skerman & Riveros 1990; Pemadasa 1990, Parihari et al. 1999) persist in the protected sites.

Thus, in both the pathways it is the herbs that dominate the youngest series, followed by shrubs. The appearance of tree species in the 2nd year without dominating is widely documented in temperate old fields, USA (Buell 1970; Pickett 2001) and tropical Africa (Swaine & Hall 1983). The secondary species & primary forest species become common only in the beginning of the mid- successional stages, similar to findings in Bolivia, Claros (2003) where woody plants recruit continuously but dominate only later stages due to different rates of growth and life-span. In another tropical dry forest (Aide et al. 1996) found shrubs and trees dominating after 20-30 years. This indicates that other species are not available in the immediate vicinity of the sites or the site conditions are not conducive till that point in succession. Species within the immediate vicinity of the sites are the ones to colonize early and late species might be slow in arriving if sources of propagules are distant from new sites (Platt & Connell 2003). According to Pickett et al. (2001) ‘volleys of invasion’ by propagules of species were necessary before they were successfully recruited and established. It is clear that the succession seen occurring in this study, is the facilitative type with herbs leading to shrubs and trees in 20-50 years time (Clements 1916; Connell & Slayter 1977; Platt & Connell 2003; Kobayashi 2004), and
there is a sequential replacement of species (Fig. 1 & 2, Table 1 & 3), in agreement with the common trend of succession seen (Huston & Smith 1987; Mc Cook 1995), but favouring nucleated succession in open areas where vegetation occurs only in patches.

In this study it is the uniform shade and amelioration of soil fertility by the leguminous *Acacia auriculiformis*, that makes widespread establishment of *Memecylon umbellatum, Ixora pavetta, Hemidemus indicus* and *Tarenna asiatica* possible in the 30 year protected sere. Even after 50 years, the clumps in open areas cover only 24% of the studied area, while the directed sere of 30 years recorded 400% cover (Table 8). Shading is thus the major factor influencing development of the primary forest species (Tilman 1985). There was higher levels of organic matter content in the older sere, especially the protected seres, but there was no statistically significant soil amelioration (Table 12 & 13).

This study does not agree with the 'Initial floristic composition' proposed by Egler, since the initial floristic composition has not been the determining factor in this study, even though there are many common species found in the protected and open areas. As the study is based on chronosequences, it is not possible to verify the occurrence of 'volleys' (Pickett et al. 2001), or 'relay floristic' (Clements 1916). However, considering the difference in species that dominate the two pathways, grazing, as a major driving force in the landscape's ecology is indicated (Connell & Slayter 1977). Many species of grasses and herbs are distinct in the two pathways, while common species show different dominance. Species common to both type of pathways, are prostrate due to trampling in
open areas. Herb species specific to open area have hairs, and shrub & trees have spines & thorns as protection against herbivory.

The log normal rank abundance distribution shows that the community assemblages are more even in the open landscape and the early successional stage of the protected areas (Fig. 3). No single species is dominant and there are large number of factors that determine the distribution of species. The log series distribution in the mid-successional stage of the protected areas shows dominance by few species as well as the importance of one or few factors. In the 12 year sere *Sehima nervosum* dominates. In the 30 year it is *Memecylon umbellatum* that dominates, and in this case it is shade that is important. (Mugurran 2004).

**Convergence to the climax**

The similarity matrices (Table 4, 5 & 6) and PCA (Fig 6 a & b, 8) too support a change of vegetation type from the earliest sere to the oldest sere studied, in both the pathways. The lack of similarity between the oldest plots and the forest which is dominated by primary species, in 30-50 years is in keeping with other studies in TDF in neotropics, that have found no convergence after 40 years (Aide et al.1996) or in 45 years (Colon & Lugo 2006) in Puerto Rico. Aide et al. (1996) estimated that more then 100 years were necessary to recover the original composition, and vegetation in early stages in recovering forests would be different and Lebrija-Trejos et al. (2008), estimate a time between 75-150 years for convergence. Light demanding trees were the dominant species even after 50 years in montane forests of Hong Kong (Zhaung & Corlett 1997) and a
closed canopy of shrubs in 20 years resulted in sub-alpine Papua New Guinea, in the absence of disturbance (Corlett 1987).

Given the polyclimax of Tropical dry evergreen forest and scrub (Champion and Seth, 1968) which exists in the region, the succession could also be in continuum with Tropical dry evergreen shrub (TDES) and not Tropical dry evergreen forest (TDEF), due to the disturbed nature of the site compounded by the fragmented nature of the TDEF. A recent review of the TDEF in the Coromandel coast, covering 75 fragments found significantly low similarity among the fragments, with varying species composition (Parthasarathy et al. 2008). So it is possible that the low similarity in species composition between the oldest seres and Puthupet is because it is not the source of seeds for the sites studied, though the primary forest species recorded in the seral stages have been documented as component species of the TDEF in other sites (Venkateswaran & Parthasarathy 2003, Reddy & Parthasarathy 2006). The increasing similarity within plots of the same age in the protected pathway is expected (Myster & Pickett 1990), though the same is not true for open plots.

Comparing the oldest seres, the life-forms seen in protected sites resemble the forest more than the open areas that are dominated by shrubs, along with early seral species like herbs & grasses even after 50 years. The height analysis shows that the trees in protected areas (3m) are closer to the forest (5m), with trees in open areas (2 m) being short in stature (Table 7 & Fig 9).
Structural analysis of vegetation

Height analysis

Increase in height of vegetation with time seen in two pathways is expected (Huston & Smith 1987) (Table 7 & Fig 9). One reason for the difference in height between the two pathways is due to the difference in species found and due to the prostrate habit of many of species in open landscape, which would grow erect and tall in the protected sites like Sehima nervosum, Heteropogon contortus, Aristida setacea & Rostullaria simplex. Browsing also stunts trees like Securinega leucopyrus & Azadirachta indica. The dominance of shrubs in the open sites, instead of trees, as in protected areas influence woody species height. The height difference of 100% could also be an indicator of better nutrient and water availability in protected areas (Fig 15, Table 12), even though the difference is not statistically significant.

The importance value of the different kind of successional tree types, clearly demonstrate the dominance of primary forest species in protected areas, and the population structure showing a reverse J shaped structure, with the largest individuals in the youngest size classes shows continuous recruitment found in both the pathways, though the community structure and vegetation stand structure of the directed patches closely resemble the forest.

Dispersal modes

The mode of seed dispersal is similar in the first three seres in both pathways. In the oldest seres, while endochory followed by anemochory is the dominant mode,
mymechory needed for grass and ectochory showing the presence of grazing animals are seen only in open seres (Fig. 16). The seed dispersal modes seen in the study agree with those found in Colombia Amazonia, where autochory (60%) was the dominant dispersal mode in open herbaceous areas with anemochory (40.2%) and zoochory (37.8%) being dominant in forest shrub vegetation (Arbelaez and Tarrado-Rosselli 2005). Zoochory (69.2%) was the most important dispersal mode for two TDEF forests species (Swamynathan & Parthasarathy 2005), and in both types of oldest seres explaining the presence of TDEF species like Memecylon umbellatum, and Ixora pavetta after 50 years in the open and the presence of Clausena dentata, Disopyros ferrea, Disopyros ebenum, Walsura trifolia, Psilanthus wightianus, Glycosmis pentaphylla and Manilkara hexandra. While Chloroxylon swietenia and Gymnema sylvestre found in the 50 year clumps and Hemidesmus indicus, Ichnocarpus frutescens and Tylophora capparidifolia in the 30yr protected seres are anemochorous. Thus long distance dispersal is more common latter than in the earlier stages, making the immediate areas around the disturbed sites the seed source for the earlier seres (Nascimento et al. 2006).

Geographical distribution of species

The protected seres encourage the growth of Asian and old tropic species, while species with pantropical distribution are common in the open seres. In the oldest seral stages considered, the number of species that are restricted to Peninsular India and Sri Lanka is 10 in the open seres, and 20 in the protected. While some studies (Kellman 1980) report the widespread occurrence of species with wide geographical distribution, Corlett (1992) found that in Hong Kong, species with wide geographical distribution were restricted to
open or recently disturbed sites, without significantly invading secondary grasslands and shrubland.

In the present study cosmopolitan species are found in the initial three protected seres, but more number of such species occurs throughout the spontaneous succession, even upto 50 years. So directed succession discourages the establishment of 'weedy' species and is more conducive for the establishment of local species.

**Effect of grazing**

The effect of grazing is seen in the decrease in diversity at the level of species to families in the open seres. The protected areas have species 123 species from 111 genera, in 41 families, while open areas have 109 species from 97 genera in 36 families (Table 2 a & b) similar to Sahel, in Africa (Heurmanx 1998), where grazing decreased palatable species, upto 30% and increased the dominance of only a few species. Many studies have observed that, at moderate intensities, species richness is high as it reduce competition by the dominant species, but under heavy grazing species richness falls (Singh & Mishra 1969; Swartzan & Singh 1974; Pandey & Singh 1992, Saberwal 1996) in India, and in Serengeti, Africa (Mc Naughton, 1979, 1993; Belsky 1992). Open area are subject to continued grazing, that increase not only recruitment but also extinction (Gibson & Brown 1992).

The protected and open areas are initially more similar 45%, but this is reduced to 27% in the oldest seres (Table 10, Fig 7 & 8), as the rate of succession is faster in areas protected
from grazing and benefiting from soil and water conservation. Woody shrubs dominate in the 6 years, with forest species appearing well established to show 9% basal area of the forests. In the open areas, shrubs are dominant only in 10 years, with forest species appearing in 50 years. Though the total species richness is more in open areas (38) compared to protected areas (30), most of the species (21) are herbaceous and shrubs. In fact, considering oldest seres, there were more trees 8 secondary and 5 primary species in open areas, with only 6 secondary and 4 primary species in protected areas (Fig 11). Considering plants ≥1 cm, the life-form composition in the oldest seres varies, with the open areas recording eight shrubs and eight trees, and the protected areas four shrubs and 17 trees species. So the secondary and primary tree species manage to recruit in the open areas, but their growth is either less or they suffer mortality preventing them from achieving girth and cover comparable to the protected areas. Similarly, herbivory was found to influence abundance, not species richness in Mongolia (Sasaki et al. 2008). Hence the protected areas show 16.4% similarity to the forest and the open areas show only 5.3% similarity to the forest.

The benefit of soil and water conservation and protection from grazing, is best seen in the development of vegetation structure ≥1 cm. Density, cover and height show significant difference between open and protected areas (Table 8). In the protected areas, density is 7 times more, basal area is 5 times more, cover is 29 times more and height is 1.5 times more than in open areas (Table 9, Fig 10). Herbivory is a critical constraint, causing a selection of plants that are better adapted to survive herbivory, as a result influencing
community structure in open areas (Tilman 1980, 1985). The difference in spontaneous and protected succession are encapsulated in Table 33.

Table 33. Effect of protection from grazing and due to soil and water conservation measures

<table>
<thead>
<tr>
<th>Attributes</th>
<th>Spontaneous/Open</th>
<th>Directed/Protected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness</td>
<td>109</td>
<td>123</td>
</tr>
<tr>
<td>Dominant life-form</td>
<td>Herbaceous</td>
<td>Woody</td>
</tr>
<tr>
<td>Woody species dominate in</td>
<td>12 years</td>
<td>6 years</td>
</tr>
<tr>
<td>Secondary species dominate in</td>
<td>50 years</td>
<td>30 years</td>
</tr>
<tr>
<td>Primary species dominate in</td>
<td>50 years</td>
<td>30 years</td>
</tr>
<tr>
<td>Seed dispersal modes</td>
<td>Endochory (63%)</td>
<td>Endochory (76%)</td>
</tr>
<tr>
<td></td>
<td>Autochory (15%)</td>
<td>Anemochory (14%)</td>
</tr>
<tr>
<td></td>
<td>Ectochory (15%)</td>
<td></td>
</tr>
<tr>
<td>Geographical distribution of species</td>
<td>Pan-tropical</td>
<td>Asian &amp; Pan-tropical</td>
</tr>
<tr>
<td>Similarity to forest</td>
<td>5%</td>
<td>16%</td>
</tr>
</tbody>
</table>

For trees ≥ 1cm

<table>
<thead>
<tr>
<th>Woody species of oldest seres</th>
<th>17: 9 shrubs &amp; 8 trees</th>
<th>21: 4 shrubs &amp; 17 trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density/m²</td>
<td>21</td>
<td>164</td>
</tr>
<tr>
<td>Mean height</td>
<td>~ 2m</td>
<td>~3m</td>
</tr>
<tr>
<td>Basal area</td>
<td>14m²/ha</td>
<td>73m²/ha</td>
</tr>
<tr>
<td>Cover</td>
<td>24%</td>
<td>710%</td>
</tr>
<tr>
<td>IVI of secondary trees ≥ 1cm gbb</td>
<td>250</td>
<td>58</td>
</tr>
<tr>
<td>IVI of primary trees ≥ 1cm gbb</td>
<td>50</td>
<td>196</td>
</tr>
</tbody>
</table>
Most of the shrubs and secondary tree species recorded in open areas survive as they have thorns as defence against herbivory. The primary tree species manage to survive due to protection afforded by the thorny secondary species as the vegetation tends to occur in clumps in the oldest sere. These clumps cover 24 m$^2$ of the plots (100sq m). This is similar to results reported from an African savanna in Swaziland, where shrub encroachment increased from 2% in 1947 to 31% in 1990 and was correlated with grazing, which controlled fire frequency (Roques et al. 2001). Since grassland fires are unknown (Blasco & Legris 1973) in the ‘TDEF area’, grazing in open areas, probably aids shrub encroachment by decreasing competition from herbs and dispersal of seeds through domestic animals, as endochory (63%) and ectochory (13%) were the dominant seed dispersal (Van Auken 2000) As terrains here are poor in organic matter and dry (Blasco & Legris 1973) an increase in organic matter even though statistically non-significant can presumably aid in the establishment of trees and shrubs. Succession in the open areas is explored in detail in the next section on facilitation of this thesis.

**Resilience**

Similar to the neotropics, there are only three phases without any long-lived secondary, between the pioneer tree stage and the appearance of primary forest species (Lebrija-Trejos et al. 2008). Considering protected seres, the early stage dominated by herbs and grasses last for 6-12 years, when the mid-successional phase starts, with domination of trees. Woody species richness continues to rise till 30 years, similar to studies in Puerto Rico, where Aide et al. (1996) found species richness began increasing from 10-15 years to 40 years in Puerto Rico and, in 45 years species levels were similar to that in the forest
(Colon & Lugo 2006), The species richness of 21 recorded in protected areas is less, than
that found in Bolivia 59 species in 40 years (Pena-Claros 2003).

Density in protected areas (164/100 m²) was nearly three times that in the forest (55/100
m²). Density in recovering forests neared forest density for trees ≥1 cm dbh in Puerto
Rico (Aide 1996); and 70% in Bolivia (Pena-Claros 2003) in 40 years, so density in this
study is the highest density recorded in recovering forests. A similar trend, was seen in
the basal area of (72.7 m²/ha) found in protected areas which is 1.4 times the basal area
found in the forest (51.24 m²/ha), and is a faster recovery than reported in other reports,
where basal area was similar to forests in 40-45 years (Aide et al. 1996; Ruiz et al
2005; Toledo & Salick 2006). Height increased with age, and was 65% (3 m) of the forest
mean height (5 m). The species richness (21) was 88% of the forest species richness (24)
and increasing as found in Puerto Rico (Aide et al. 1996), in Bolivia (Pena-Claros 2003;
Toledo & Salick 2006), and in Caribbean forests (Ruiz et al. 2005). So the recovery rate
of the protected areas is better or comparable to the neotropics, as the time scales of 40-
45 years considered is similar to the present study, in terms of density and basal area, but
not height or species richness.

The forest recovery in open areas of density 21/100 m² or (38%), height 2m or (48%) and
basal area 14.33 m²/ha or 28% is far below the recovery rates in other TDFs. See
Appendix B for species comparison.
**Interspecific associations**

The trend of increasing number of interactions for both herb herbaceous and woody species, is in keeping with the first hypothesis of Myster and Pickett (1992). The number of interactions among herbaceous species was 703 and 1216 and interactions among woody species were 106 and 146 in open and protected pathways respectively. So this proves that species with a broader niche have more interactions, than later successional species, proving the second hypothesis of Myster and Pickett (1992). However the number of interactions are less in the forest, suggesting that Greig-Smith’s theory of pioneer-building-mature phases for interactions. As a result of grazing, the number of interactions of herbaceous and woody species are 1.7 times and 1.4 4 times more in protected pathway than in the open pathway, agreeing with the study by Smith (1954).

The overall community level interaction in all the seres of both pathways are positive and significant. Facilitation is indicated as the net force influencing succession (Clements 1916; Connell & Slatyer 1977).

Considering, species involved in interactions herbs like *Alysicarpis monilifer, Rostellularia simplex, Blepharis repens* and *Heydotis puberula* are important till the 10th and 12th year sere. *Aristida setacea* is the most interactive grass species, followed by *Sehima nervosum* and *Heteropogon contortus*. In the 10th and 12th year sere., *Heydotis puberula* and *Desmodium trifolium* are the common interactive plants. *Acacia holoserecta* and *Azadirachta indica* are in interactions with herbs and grasses, though it is
only in the oldest seres that woody species are involved in ten interactions or more, since their number is less and they are scattered. *Acacia auriculiformis* the exotic that was planted was interactive in open and protected areas. *Memecylon umbellatum*, which is the dominant species in protected areas is also important.

In the first two seres it is the herbs and grasses that are interactive. The shrubs though they are increasingly abundant in the third open and protected seres, they influence community structure only in the oldest seres. In the protected areas, the interactive species are trees like *Acacia auriculiformis*, and *Phoenix pusilla*, while in the open areas it is four shrubs and two trees *Acacia auriculiformis* and *Azadirachta indica*. The paeking of co-variations till later in the protected areas, again indicate strong interactions that sustain longer (Smith 1954).

**II. Facilitation experiment**

*Phoenix pusilla* tends to form intra-specific clumps, as the palm needs shade during the younger ontogenic stages (Kinchal & Parthasarathy 2008a) for recruitment. These clumps of thorny domed shaped palms, grow progressive larger (clumps large as 25 m² are common), and neighbouring clumps coalesce to form bands. This feature of the Phoenix *pusilla* makes it an excellent nurseplant, helping it to ameliorate microclimatic conditions and provide protection against herbivory (Aguiar & Sala 1999). Similar nucleated succession of woody species has been reported from all kinds of ecosystems, the sand
dunes (Yarranton & Morrisons 1974; Frank 2003), savannas (Archer et al. 1988) and old field (Li & Wilson 1998).

The results of the spatial analysis and experiment show that *Phoenix pusilla* is indicated as the prominent habitat modifier in the study sites facilitating other plant species directly and indirectly. There are more species found associated with it than in the open interspaces or the other dominant associate *Dodonea viscosa* (Table 26). 11 primary and two secondary species were found associated with it (Table 25a). Similarly *Olseya tesota*, a nurse plant has been associated with higher species diversity in the Sonoran desert (Suzan et al. 1996). Frank (2003) found more plant abundance correlated with nurse plants than in open areas in primary sand dune succession in Florida. Cavieres (2006) found cushion plants facilitating 26 plant species in the Andes, Chile.

Some of the primary species recorded with *Phoenix pusilla* were also recorded with *Dodonea viscosa* Most of the secondary trees species that are shade intolerant, do not need any facilitation and are therefore more common in the open, except *Azadirachta indica* and *Bridelia crenulat*, which were found to be facilitated by *Phoenix pusilla*. It is the shade-tolerant primary species that require facilitation (Gomez et al. 2004), that are associated with *Phoenix pusilla*.

The experimental findings show that both soil and micro-climatic amelioration is effected by *Phoenix pusilla*, similar to Gomez et al. (2005a) who tried to determine importance of canopy vs soil effect (Table 27).
Though higher organic matter content found under *Phoenix pusilla* is a considered a characteristic feature of nucleation (Schlesinger & Pilmanis 1998; Aguiar & Sala 1999; Casal 2001), there have been studies which report no greater nutrients under nurseplants like Gomez et al. (2005a) who found that nitrogen, phosphorus, and organic matter were not greater under nurseplants, but potassium was. Martinez (2003) reported temporal variations in different nutrients nitrogen, organic matter and phosphorus around the year. Nutrients in a patchy area are abiotically and biotically redistributed; abiotically, mainly by wind and water and by accumulation of litter from the nurse plant, and biotically by relocation of nutrients from the surrounding area and the depths of soil by the plants roots and due to the increased presence of soil microbes under shade (Gutierrez & Jones 2006). As a result of the humus accumulation the soil crumble is improved enabling better germination than in dry compact soil in the bare patches (Gutierrez & Jones 2006).

The soil temperatures recorded were 1.35 times higher in the interspaces, than under the *Phoenix pusilla* (Fig 22). Martinez (2003) too, found that the soil temperatures but not air temperatures were lesser under nurseplant *Chamaecrista chamaecristoides*. while Gomez et al (2005a, 2008) found both air and soil temperature were less under the shade of nurseplants than in bare interspaces. Soil temperature is very important to determine the health and growth of the newly germinated radicle, which can dry fast. Holmgren (1997).

The higher water content in the present study is supported by similar findings from Frank (2003) but not Gomez et al. (2005a, 2008). The shade of the plant reduces soil
temperature and thereby reduces soil evaporation of soil moisture, that makes more water available to the plants (Shreve 1931; Holmgreen 1997). In addition evapo-transpiration of young seedlings is reduced, benefitting its growth (Franco-Nobel 1989).

Many studies have found that photosynthetically active radiation is better suited to plant germination under shade than in bare areas (Casal et al. 2001), and is lower under nurseplants than in the open areas (Banuet 1991; Martinez 2003). Though Gomez et al (2006) found lower irradiance under shade, the response of the different species depended on their ecological, morphological and physiological characteristics (Fig 20).

The interaction of less radiation, better soil structure and fertility is reflected in the germination of *Walsura trifolia* and *Diospyros ferrea*, in our study. Five times as many seedlings were established under *Phoenix pusilla*, than in open interspaces (Fig 22). Higher seedling germination and emergence is reported from the inter-tidal regions in New England (Bruno 2000), in Mexico under the endemic shrub *Chamaecrista chamaecristoides* (Martinez 2003), during sand dunes succession in Florida (Frank 2003) and of *Acer opalus* under Mediterranean shrubs (Gomez et al. 2005c).

Of the 14 seedlings that emerged in the open interspaces, two were found dry and two very missing, making it difficult to comment on the cause of their mortality. The experimental design does not permit us to determine whether the mortality of seedlings (Fig. 22) was due to abiotic stress (summer heat and resultant water stress) or biotic stress (herbivory). But as 70% of the seedlings that emerged in open interspaces did manage to
survive, it is germination that is indicated as the crucial stage in determining the seedlings numbers.

Surviving *Walsura trifolia* seedlings were nearly twice as higher under the shade of *Phoenix pusilla* than in the open interspaces (Fig 23). Mandujano et al. (2002), found that three species of cacti were bigger in size under nurseplants than in bare spaces. Saplings planted under shrubs showed better growth in Spain than when planted in the open, even after four years, with no competition from the nurseplants (Castro et al. 2004). Reducing radiation has been shown to promotes better seedling growth, as excessive radiation in open, hot and dry microsites can photo-inhibition of photosynthesis in many plant species (Valladares 2003; Gomez-Aparicio et al. 2004).

Since both study sites are many kilometers away from nearest remnant forest patches, arrival of the progagules to the site is most probably by birds given that 70 % of TDEF species are zoo-chorous (Swamynathan & Parthasarathy 2005). *Phoenix pusilla* has drupes, that probably attracts foragers, who disperse seeds by defecation or regurgitation (Verdu & Garcia 1996; Archer 1988; Aguilar & Sala 1999).

That *Dodonea viscosa* is a nurse plant, needs to be substantiated by experiments showing how it operates, as this information can help us understand how it facilitates the primary tree species recorded with it (Wright & Jones 2006).
A total of 112 species - 77 tree species >10cm gdh (Mani & Parthasarathy, 2006) and 35 liana species >1cm dbh (Reddy & Parthasarathy 2006) - have been recorded in the fragmented TDEF on the Coromandel coast. However, the number of woody species in a fragment ranges from only 6-36, with a significant difference in species composition between the fragments (Parthasarathy et al. 2008). Since Phoenix pusilla is associated with 13 primary forest species of the TDEF, Phoenix pusilla can be called an ecosystem engineer and a foundation species (Dayton 1975; Jones et al. 1994, 1997), with the landscape engineered by it comparable to the average species richness of the fragmented TDEF. The TEK claim that Phoenix pusilla is the nurse plant that initiates nucleation in and degraded landscape can be accepted validating the Irulas’ understanding of the concept of nurse plant and of ecological processes (Gadgil et al.1993; Birkes et al. 2000).

This study is in keeping with other studies (Lugo 2002; Nagendran et al. 2008) that have discovered regeneration of forests in populated landscapes simultaneously with forest degradation. The nucleated vegetation patches in our study, which are 50 years old, cover up to 30% in areas subject to regular grazing and resource removal (Kinhal & Parthasarathy 2008b). However, these patches are generally regarded as scrub. Their role, as possible refugia for shade-tolerant forest species and needs to be highlighted both in research and restoration, especially since the TDEF fragments have varying species composition (Parthasarathy et al. 2008).

The nucleated vegetation patches are widely distributed in populated rural area, in revenue land in villages and private properties, and since are not currently included as
forest habitats. Therefore, the role and contribution of these patches in regional ecological processes in the fragmented TDEF landscape, has never been considered. It is necessary to understand the processes of natural resilience of ecosystems for better landscape management (Lugo 2002). These patches have existed with zero afforestation effort, are entirely spontaneous and have a widespread though scanty distribution. A quantitative analysis of these patches is necessary to examine the role these patches may have in providing connectivity between fragments of TDEF, by acting as dispersal sources to decrease the effect of fragmentation (Welgand et al. 2005). Existing patches of nucleated succession should be protected to conserve species populations that have already regenerated outside forest fragments, and if possible, set aside for regeneration of the whole forest ecosystem.

**III. Phoenix pusilla population study.**

The results of Mantel tests revealed that in initial stages -seedlings, saplings and juveniles- Phoenix pusilla preferred (though not significantly) low light intensity or shade. That male palms, showed positive though non-significant preference for light, and female palms a significant correlation with light, signifies that female adults developed in microsites with high light intensity, indicating at least a partial niche differentiation between sexes. Clearly female plants have high light needs for flowering and development and ripening of fruits (Meagher 1981; Clark & Clark 1987).

This partial niche differentiation explains the observed sex-ratio, with the highest numbers of female Phoenix pusilla in open area with high light intensity.
(mean=38415.34 lux ± 15645.07 S.D.) and female biased sex ratio (male:female) of 1:3, compared to the male skewed sex ratio (male:female) of 1.28:1 and 1.33:1 in the moderate and partial shady environments of the plantation (mean lux = 11849 ± 8924.63 S.D.) and savanna (mean lux=13140.60 ± 13032.81 S.D.) respectively; adults were totally absent in the canopy-closed under-story of tropical dry evergreen forest (mean lux = 3644.83 ± 2798.01 S.D.). The high female: male sex ratio found in the open area is typical of female adults exploiting favourable sites (Onyekwelu & Harper 1979; Clark & Clark 1987), with males more abundant where conditions are less favourable (Meagher 1981; Ramadan et al. 1994) as was found here in the savanna and plantation. The reasons mentioned in literature for the male biased sex ratio are, true genetic sex ratio (Barlow & Weins 1979), differences caused in flowering or survival (Meagher 1981) or microsite preferences (Meagher 1980). Meagher (1980) found differences in the spatial distribution of Chamaelirium luteum along environmental gradients and suggested that it is a byproduct of sexual dimorphism due to varying physiological demands. This brings about differences in the ecological tolerances in the sexes on the scale of microsites. The preferential difference for light and the varying dispersion of abundance of adults seen in Phoenix pusilla supports this theory.

There were more of younger ontogenic stages in plantation and savanna, whose semi-shady environment favors the establishment of seedlings and saplings than open area. The open area with high light intensity and heavy grazing resulted in few seedlings surviving to the sapling stage but had more adults than savanna and plantation, due to the higher light intensity that adults need for their growth and fecundity (Table 28).
population structure (Fig 24) of delayed reverse J structure in *Phoenix pusilla* in all habitats except the open area, indicating highest mortality in the youngest classes, and the density distribution of the classes, is in agreement with that observed in other tropical palms (Van Valen 1975; Pinard 1993; Silva Matos et al. 1999; Souza & Martin 2002).

The Mantel test results which show abundances of seedlings and saplings are not correlated with the female adult abundances, indicate survival of seedlings away from the mother palm. This agrees with dispersion in the Brazilian acaulescent palm *Attalea humilis* (Souza & Martin 2002), and *Euterpe edulis* (Silva Matos & Watkinson 1998), but not *Iriartea deltoidea*, in which, Svenning and Balslev (1999) found their Mantel test showed a strong correlation between seedlings and adults.

The highest periods of mortality resulting in a sharp decrease in the number of younger individuals in the *Phoenix pusilla*, when considered in conjunction with the increasingly clumped dispersion seen from seedlings to juveniles in the savanna, plantation, and Puthupet forest shows that palms are concentrated in favourable microhabitats indicating density-independent mortality. The favourability of micro-habitats could be due to light, and availability of water and nutrients. Microhabitat heterogeneity could explain the correlation of juveniles and adult males to females, especially since males show positive though not significant correlation with light intensity. Competition among adults produces less degree of clumping in the savanna and plantation. Dispersion in other palms, with aggregation of later stages- juveniles- in favourable habitats (Silva Matos &
Watkinson 1998; Barot et al.1999) and more diffuse clumps in the adults (Souza & Martin 2002) is in agreement with our observation in all the habitats.

Since the ten individuals of *Phoenix pusilla* occurred only at the edge, and there are no adults in the tropical dry evergreen forest, we hypothesize that *Phoenix pusilla* occurs due to mass effect in this particular habitat and is dependant for recruitment of new individuals from the neighbouring matrix (Shmida & Wilson 1985; Svenning 1999).

Svenning (2002) found that in even shade-tolerant understory palms, like *Geonoma macrostachys*, low illumination microsites could result in population level consequences severe enough to lead to local extinction.

In the open area, indicating preference to favourable sites, *Phoenix pusilla* is usually seen in aggregation with other plant species in a surrounding matrix of bare area. Consequently areas of shade are localized, favoring clumped seedling establishment. In these aggregates, *Phoenix pusilla* showed decreasing densities through the ontogenetic stages as well as less clumping indicating that density dependent forces are also acting here. Female palms are significantly clumped again due to higher densities. As light is not a limiting factor in this habitat, factors like better nutrient availability in aggregations (Barot et al.1999) may be responsible for the clumping.

Light is an important factor for plant size increase in plants (Chazdon 1992), but the plant size (number of live leaves) and reproductive activity (number of inflorescence) of adult male and female *Phoenix pusilla* was not influenced by light. There was significant
correlation between plant size and inflorescence production in case of male but not female palms (Fig 25). Clark and Clark (1987) found a similar correlation of reproductive activity and plant size but in both sexes of Zamia skinneri. It can be seen (Table 32), that in female palms the number of leaves increased from plantation to savanna to open area, but reproductive activity / number of inflorescences per palm decreased from plantation to savanna to open area. In the male palms, plant size and reproductive activity increased from plantation to savanna to open area, reflecting the positive correlation of plant size and inflorescence numbers in male palm.

The correlation of abundances of adult female palms to light, cannot be explained with our data either by its influence on plant size or flowering. The importance of light would have to be investigated for fruiting to explain its influence on the observed dispersion of the adults. Since the open area has the highest adult population, the largest plant size of the adults as a measure of favourable habitat (Ramadan et al. 1994), as well the presence of the highest female-based sex ratio which usually happens when the conditions are favorable (Meagher 1980), we hypothesize that open areas are the most suitable of the four habitats studied for Phoenix pusilla. However, further studies on pollination and fruiting are necessary to conclude in which habitat Phoenix pusilla is most productive.

IV. Economic study of wasteland species

Most of the species contributing to the biodiversity of the agricultural fallows are of wide geographical distribution. Even the trees are mostly Asian. But though the species are not unique to the region as expected (Kellman 1980), their economically value for the local
population, as recorded by the Pitchandikulam Bioresource Project, can be judged from the fact that nearly 70 species recorded are used, a majority for medicinal purposes (Appendix A) based on traditional healing systems. Thus the ‘wastelands’ make an important contribution to the health of people in the rural areas, where modern health services are inadequate.

Given the importance of the wastelands/common community resource areas to the people, the picture of them being an economic and ecological waste should be reassessed. Any attempt to use these lands for ‘development’ schemes, a recurrent trend (Singh 1985), should be re-evaluated in the light of the dependence that the poorest sections of the rural population have (Jodha 1985; Berkes et al. 1998) on the local biodiversity. Development agencies will find it harder and more expensive to provide substitutes for the food, medicines, fuels, fodder and other environment services like erosion control, clean water that these community resources offer currently (Kaimowitz & Sheil 2007).

**Recommendations for management**

Directed succession studied here has produced one the fastest recovery rates in TDFs so is the ideal solution to restore the TDEF. However, the benefits from protected areas come at the cost of excluding access to usufructs benefits that people coupled with expenditure that has to be incurred for growing nurseries, planting and guarding sites. Since resources are scarce and the available money has be used efficiently (Castro et al. 2002) spontaneous succession though only 30% as efficient as directed succession is
useful as nucleated succession by which it occurs is an common occurance (Kellman 1980; Esquivel et al. 2008). The resultant scrub that it produces in densely populated areas need to be protected, due to the role they can play in conserving primary forest species population without a need to discontinue or disturb the existing livelihood benefits that local communities derive from these landscapes. Semi-natural habitats like hedges or agroforestry coffee plantations are increasingly being seen as a possible and viable means of conserving populations of many species (Bhagawat et al. 2008), so a regional conservation for TDEF should take into consideration these areas existing outside formally protected areas.

Therefore clear cutting of existing vegetation however thorny, to make way for plantations should be avoid as the secondary species found here are adapted to thrive in the dry and barren conditions found in wastelands. The role of shrubs in facilitating secondary succession especially in open dry areas is well established (Gomez-Aparicio et al. 2004). The wide geographical distribution of secondary tree species recorded, which are either of pantropical or Asian distribution (Appendix A), can be an asset as they can easily be used everywhere in lowland India and Asia for restoration of forests. Management and choice of species in restoration in human dominated land need to retain multiple values of productive land and prevent any further loss in biodiversity by diversion of other natural habitats like forests (Daily 1995).

*Phoenix pusilla* an endemic thorny acaulescent palm was identified as a possible nurse-plant with the help of TEK from a tribe Irulas. *Phoenix pusilla* has multiple uses, its fruits
are edible, its leaves are used for making basket and mats, and the entire shoot tip is used as fuel in lime making (Gamble & Fischer 1935; Basu & Chakravety 1994), so it is common to see leaves cut or the whole plant uprooted. Being thorny and locally abundant, it is considered a weed, so Phoenix pusilla is often cleared away. However, Phoenix pusilla is endemic to the Coromandel coast, found only over few hundred square kilometers, and therefore deserves to be conserved. In addition, the possible overexploitation and destruction of this ecosystem engineer requires more attention because the consequences extend beyond their own decline to affect the rest of the ecosystem (Coleman & Williams 2002).

Since the range of the endemic Phoenix pusilla overlaps the distribution of TDEF, it can be used in restoration of this rare forest type. Selection of future sites for restoration or conservation on the Coromandel coast could focus on Phoenix pusilla dominated landscapes, to catalyse the project. Additionally, sowing seeds of forest species under Phoenix pusilla, can be undertaken if necessary to enrich the area. Integration of spontaneous succession, with the right kind of intervention, at the right phase of a project, can ensure its efficiency (Sprach et al. 2001). So, it makes economical and ecological sense to integrate nucleated vegetation into conservation and restoration projects, since scarce resources can be used to cover larger areas (Castro et al. 2002).

The choice of the habitat to be restored is as important as its size. Maintaining corridors or landscapes with patches in a matrix of lesser suitable habitat is in many cases a more realistic goal for many species survival, though not all of them (Huxell & Hastings 1999). Populations in fragmented landscapes might be structured as metapopulations, in any
case, regional ecological processes are important for plant distribution (Ehrlen & Eriksson 2003; Melbourne et al. 2004). Therefore successful restoration and biodiversity conservation should have a regional plan, rather than focusing on a specific site. In which case, the selection of sites or ‘mitigation banking sites in a stepping stones manner’ would allow the persistence of populations in isolated populations (Huxell & Hastings 1999). Since maintaining viable populations in fragmented landscapes depends on an interaction of dispersal, connectivity, landscape structure and scale, mitigated sites can be important in providing connectivity and maintaining numbers (Henle et al. 2004).

Managers of restoration and conservation projects need to be aware of the potential of nucleated succession in reintroducing forest species, as well as the store of information that TEK - based on accumulation and transfer of information for generations- can provide them. Positive interactions are being included into ecological theory and restoration projects only in the last six years (Bruno et al. 2003; Castro et al. 2002) but TEK of Irulas, shows that it is common knowledge among them. It has been found that when natural resource and landscape management projects integrate TEK with scientific guidelines, they are more acceptable to local stakeholders and likely to be effective even after the donor agencies quits the project (Garcia & Lescuyer 2008), giving restoration and conservation a better chance.