II. REVIEW OF LITERATURE
SUCCESSION is one of the most important directional forces driving vegetation (Horn 1974). Change in species composition and processes, of communities over time is known as ecological succession (Van der Maarel 1996; Singh et al. 2006). Most of the work on succession concentrates on vegetational development. There are three main types of successions depending on the history and initial conditions of the landscape. Succession occurring on newly exposed substrate is called primary succession, as on volcanic deposits, dune sand, and mud flats. Land that has been disturbed by event/recurring events like fire, floods, hurricanes, agriculture and pasture use, has topsoil, and existing sources for regeneration in the form of seed banks or tree stumps, and the vegetational development on it is called secondary succession. Secular succession concerns long-term vegetational changes to changes in climate covering thousands of years. (Clements 1916; Van der Maarel 1996)

Succession is an old concept proposed nearly a century ago, but has seen increasing volumes of literature produced on the subject, attesting to its importance in the current scenario of land degradation. The subject has seen many theories, models and field studies debating different points of view, and their implications for central for restoration ecology and biodiversity conservation.

It is now agreed that most of the succession seen is sequential, with one set of species being replaced by that of another which is usually longer lived, with herbaceous species
being replaced by woody species (McCook 1994). This is though by no means the only pathway possible, with cyclic succession and autosuccession/demographic being other possibilities (Huston & Smith 1987; Yih et al. 1999; Platt & Connell 2003).

Clements (1916) was the first to suggest the concept of change in vegetation. According to him the process of ‘nudation’ or formation of a bare area, was followed by ‘migration of species’, which lead to ‘ecesis’ or establishment of the species. The established species produced a ‘reaction’ by altering the habitat (eg casting shade, improving soil fertility) in which they occurred, making it more suitable for other life-forms, but detrimental to their own existence as they could not compete with the new arrivals. This produced a sequential replacement of species, with the propagules of the later stages arriving at the disturbed site by ‘relay floristics’. He considered this pattern of succession more applicable for primary succession but not secondary succession which could have a existing seed bank or root-stock for regeneration. The succession produced progressive stabilization leading to a single endpoint, a climax he defined by an association of trees that was similar to an ‘super-organism’. An important finding in his study that species interaction are facultative ameliorating soil and micro-habitat and habitat conditions for subsequent life-forms was largely ignored till the mid-eighties when the role of positive interactions began regaining focus in ecological research (Bertness & Callaway 1994; Bruno et al. 2003) as an important process to be considered during succession and with practical application in restoration of degraded landscapes (Castro 2002, 2004; Gomez et al. 2004; Brooker et al. 2008).
Clements' concept of a 'super-organism' was strongly refuted by Gleason (1926), who considered that communities were individualistic. This concept was carried further by Egler's (1954) concept of 'Initial floristic composition' where the different growth rates of species, that all occur from the initiation of succession determines succession, without leading to a single climax. Wilson et al. (1992) pointed out that there have been two interpretations of this concept by researchers through the years. In one interpretation, that they call 'complete initial floristics', propagules of all the species needed for succession are widespread and so available at every site in an area that experiences disturbance, as ascribed to by Connell & Slatyer (1977), Whittaker (1989), Whitmore (1989) and many others. The other is called the 'pre-emptive initial floristics', where the species that are present initially, dominate succession and influence its course by pre-empting other species. According to this interpretation, a different set of initial species may be present on other sites. The two differing interpretations have important implications for land management.

Pickett et al. (2001) studying succession in the Buell succession found that woody species appeared early in succession, but were not able to establish successfully. Therefore 'volleys of invasion' by the same species were necessary before the later successional species could establish in a site.

Besides the timing of the propagules' arrival at the site, the life-history traits of the species were also considered important to explain the sequence of species normally seen. Different strategies, of life expectancy, size, dispersal, growth and survival of species
adapted to different points in succession were considered by Drury & Nisbet (1973). Grime (1974) described three life history strategies based on a combination of two factors stress and disturbance at different levels. Ruderals found in areas with low stress (resource availability) and high disturbance are usually herbs; stress tolerants occurring in high stress and low disturbance, are usually herbs, shrubs and trees; and competitors found in places with low stress and low disturbance, are usually shrubs and trees.

Gleason (1926), Egler (1954), Drury and Nisbet (1973) did not consider interactions between plants in their theories. Tilman (1985) proposed the resource-ration hypothesis that considered competition for resources and tradeoffs in life-history traits in plants to deal with resources. If these resources are inversely proportion as nitrogen availability and light intensity are, then sequential replacement of species occurs, without saying how the resources change.

Huston & Smith (1987) too proposed a competition model for resources but based on individuals. They made no apriori assumption of correlation of life-history strategies to different points in succession, and took into account that many resources have been proved to be inversely correlated in their availability. They stated that when plants are adapted to exploit one set of conditions (resource availability or environmental conditions) and cannot compete in other conditions, plants have inversely correlated traits and this produces sequential replacement. Divergent, convergent, cyclic and suppressive succession are possible with different combination of life-history traits. Their model without explicitly stating it, considers that the change in conditions is brought about by
the plants themselves, thus explaining the change in environmental conditions and species sequence seen usually in succession.

Horn (1974) described succession as a plant-by-plant replacement process based on life-history traits of size, age, growth rate of establishment and shade tolerance, without considering species interaction. Pickett (1976) expressed the same idea genetically, stating that it is important to maintain the traits that allow it occupy a point in the continuum of conditions that characterize succession but also have some variability to survive in new conditions.

Connell and Slayer (1977) considered the role of interactions as central to the process of succession and proposed three different possibilities facilitation, inhibition and tolerance and their model has been the most influential since Clements' concept (1916). Many researchers now try to determine the pathway that predominates a landscape before recommending appropriate management practices for forestry or restoration (Kobayashi 2004). Walker and Chapin (1987) though consider that forces cannot be segregated into three parts, and that more than one interaction maybe important in any succession, with facilitation more important in the initial phases and competition more widespread later. They considered biological interactions important to determine not the outcome but the rate of succession.

Rejmanek and Leps (1996) found that a particular association could also change from negative to neutral to negative again. Brooker and Kikividse (2008) stress the need to
differentiate between the intensity of competition, which is its absolute impact, and
importance, which is its impact relative to its environment. So even if competition or
negative interactions are detected it is necessary to determine its importance.

Greig-Smith (1952) interpreted the ‘super-organism’ concept of Clements (1916) as
impling “direct interactions between individuals both of the same species and different
species” and studied pairwise interaction to determine if the interactions were more in
the climax. He found that the secondary forest had more positive interactions with the
least in the primary forest. Focusing on species interactions, many studies have tried to
quantify the interactions, and study the trend in change of the type/sign (positive or
negative) through succession.

Greig-Smith (1952) proposed the pioneer-building-mature phases for interactions.
According to this hypothesis, during the pioneer stage there is small scale heterogeneity
and the dispersion of species is random. In the building phase, due to reproduction,
grouping of plants occurs, so there are more number of interactions found. In time these
patches grow and coalesce, so the distribution of individuals is random again. Greig-
Smith (1952) formulated this hypothesis based on a study of chronosequence of tropical
forests. The recovering forest aged 15 years had the most number of interaction, the
younger forests less, with the pristine forest having the least number of interactions-all of
which were positive.
Myster and Pickett (1992) formulated three hypotheses of which two are based on the findings by Bazzaz (1979) and Parrish and Bazzaz (1982) of competition in early stages of succession and the prevalence of broad niches for early successional species and specialized niches for the later successional species. (1) There should be more interactions and increase in intensity of interactions with time and (2) there is more competition among annuals and biennials compared to perennials. (3) Abundant native species are involved in more interactions compared to exotics, since abundant species may be functionally dominant and interacting (Crawley 1986).

Testing these hypotheses in the old field Buell succession in USA, Myster and Pickett (1992) found no proof for the first hypothesis, as the number of interactions decreased over 18 years. There was proof for the second hypothesis, as there were more interactions between annual and biennials than among perennials and there were relatively more positive interactions than negative interactions. It was the exotics that were more abundant and involved in more interactions; in the later series when the native species increased in abundance they were together in more interactions.

Tilman (1990) considered herbivory as an environmental factor on par with nutrient and light availability, that determines trade-offs in competitive ability in plants that can influence the course of succession. Interspecific associations within plant communities are a result of aggregated populations, which result as a product of reproduction (vegetatively), symbiosis/positive or micro-habitat heterogeneity like soil, topography, light etc. (Smith 1954). Comparing pairwise interactions she found that the number of
interactions were decreased by grazing, as grazing pressures eliminate more favourable micro-sites and make the habitat more uniform, with a subsequent break down in interactions.

Similarly Gitay & Wilson (1995) found that grazing increases heterogeneity at (0.1 m x 0.1m) scale, that is the average size of bite of herbivores, but decreases heterogeneity at larger scales. Studying associations in landscapes – aged 1-28 years- protected from fire and grazing, they found that the interaction pattern followed the pioneer-building –mature phases of Greig-Smith (1952), as a result affecting community structure.

Positive interactions in particular, as an important ecological process in stable and successional communities are increasingly documented, in contrast to early ecological schools of thought which concentrated on competition and consumer processes to explain the regulation of populations and communities (Bertness & Leonard 1997; Stachowicz 2001; Brooker et al. 2008).

Positive interactions can create new habitats, in which many small scale positive or negative interactions can occur (Jones 1997; Bruno et al. 2003), by amelioration of stress. Stress according to Stachowicz (2001) is any extrinsic condition that effects an individuals survival or fitness, and can be physiological (example temperature, salinity, drought conditions), physical (e.g effects of wind, waves, currents) or biotic (competition, predation, disease). Any organism that directly or indirectly improves the environment for individuals of its own species or other species is a habitat modifier. Jones (1997)
called the process ecosystem engineering and the species responsible for it as ecosystem engineers. Many habitat modifiers which are the basis, on which entire communities are built, were called foundation species by Dayton (1975). Jones (1994, 1997) identified two types of ecosystem engineers—autogenic and allogenic. He defined them as follows:

- **autogenic** physical engineers directly transform the environment via endogenous processes (e.g. tree growth, development) that alter the structure of the engineer and the engineer remains part of the engineered environment.

- **allogenic** physical engineers change the environment by transforming living or nonliving materials from one physical stage to another, and the engineer is not necessarily part of the permanent physical ecosystem structure (e.g. beavers).

The benefits accruing from association with habitat modifiers/ ecosystem engineers can vary. For intra-specific and inter-specific individuals this may be defense against common predators or amelioration of stress by virtue of their density or creation of favourable microclimates for regeneration. The seedling and juvenile stages are the most vulnerable stages in a plant's life-history, so favourable temperature, soil moisture and fertility conditions, protection against predators provided by adults can increase the rate of survival and establishment of even conspecifics, out weighing costs of even intense competition (Bertness & Yeh 1994; Bruno 2000). Groups of individuals could withstand physiological stress better than solitary individuals in conspecifics of *Iva frutescens*, a marsh elder. The seedlings of the elder were able to survive under adult con-specifics, since the shade of the adult reduced evaporation and thus resultant soil salinity as opposed to bare patches (Bertness & Yeh 1984). Positive interactions among con-
specifics have helped in maintaining the upper inter-tidal limit of mussels (Bertness & Leonard 1997).

The idea that facilitation can benefit other species though promoted by the early ecologists has been garnering evidence only recently and its implications for the community structure and functioning are greater than intra-specific facilitations Stachowicz (2001). There can be more than one inter-specific habitat modifier or ecosystem engineer, whose effects may be small, and be practically indiscernible or significant enough to create new habitats (Jones et al. 1994; Jones et al. 1997). The multiple eco-system engineers sometimes interact together to enhance or degrade a habitat (Braiser et al. 2008). Similar to intra-specific facilitation, inter-specific facilitation too occurs by providing refuge from predators, nutrient transfer, trophic facilitation and protection from competition.

Protection from predation results, when plants in marine and terrestrial environments suffer less herbivory and increase fitness by growing with species unpalatable to the herbivore (Atsatt & Dowd 1976). Insects live on plants that have chemical defenses (Bernays & Graham 1988). Trophic facilitation can occur through many specific plant–animal mutualisms like pollination and seed dispersal. When the plants are keystone species like figs, a breakdown of the fig-figwasp mutualism can have important ecosystem level consequences (Harrison 2000). Nutrient acquisition in plants occurs in stressful conditions by classic symbiotic associations like nitrogen-fixing bacteria in nodules of legumes and due to the presence of endo/ecto mycorrhizal fungi (Stachowicz
In fact some of these mycorrhizal fungi are the reason for the mono-dominance of certain trees species, affecting the community structure of a forest.

Ants associated with Acacia spp. protects the trees from herbivory and other competing plants and in return is provided food and domicile by the plants (Janzen 1966). Positive species-interactions have several important consequences. They can increase or decrease species diversity in a place. *Olneya tesota* that acts as nurse plant has a greater number of species growing in its shade than in bare areas of the Sonoran desert (Suzan et al. 1996). On the other hand two ecosystem engineers, the white-tailed deer (*Odocoileus virginianus*) and the invasive plant Japanese stilt grass (*Microstegium vimineum*), interact to completely alter the structure and composition of the subcanopy within northern deciduous forests in USA, thereby decreasing the number of bird species that were dependant on the mid-canopy for nesting sites and food (Baiser et al. 2008).

So though the effect of facilitation on a local scale can either decrease or increase diversity, on a larger scale by increasing spatial heterogeneity, positive interactions invariably increase diversity at the landscape level and further at the ecosystem level too (Jones et al. 1997; Wright & Jones 2007). Since the effect that ecosystem engineers have on the physical space in which other species live and these direct effects can last longer than the lifetime of the organism – engineering can in essence outlive the engineer (Hastings et al. 2007). Thus ecosystem engineering/facilitation can enhance species richness and composition stability over time to change patterns of species dominance (Badano et al. 2006).
There are variations in the strength of facilitation, which increases spatially, with thermal stress, predator pressure and lower latitudes (Bertness & Leonard 1997; Stachowicz 2000) and temporally, increases in drier years (Gómez-Aparicio et al. 2004). When stress decreases and benefits from positive interactions decrease, competition becomes more important, so mutualism and competition are a continuum of interactions (Bronstein 1994; Stachowicz 2001). However Michalet (2006), show that both negative and positive interactions can occur at the same time, with the net effect being positive in times of stress. Various factors like age of beneficiary or facilitator and the presence of above ground or below ground competition between the two can result in fitness loss for either (Michalet 2007).

The importance of stress in determining plant-plant relationships has been established and evidence of facilitative effects between plants tended to come from severe environments, such as deserts, arctic or alpine tundra systems, or salt marshes. Increased environmental severity appeared to increase either the potential for, or strength of, positive interactions, relative to negative interactions, thus shifting the observable net interactions toward facilitation in extreme environments (Callaway & Walker 1997; Gómez-Aparicio et al. 2004; Cavéres et al. 2006).

The stress gradient hypothesis (SGH) based on the model of Bertness and Callaway (1994) which includes both stress and consumer pressure as forces promoting facilitation examines patterns across gradients. Studies conducted along various stress gradients to
test this model found conflicting evidence for the SGH model. Choler et al. (2001) found that increasing altitude was associated with increasing frequency of facilitative interactions. They also found that facilitation depended on species identity and facilitated species were common at the extreme ends of their environmental tolerance and led to range expansion. Along the aridity gradient (Gómez-Aparicio et al. 2004, Agüar & Sala 1999) found nurse plants ameliorated water stress, but Tielbörger and Kadmon (2000) found that with increasing rainfall, the interactions changed from negative to neutral, and then to beneficial in desert herbs facilitated by shrubs. However, Maestre et al. (2006) found in a meta-analysis that there was no increase in either negative or positive interactions between plants in arid and semiarid environments.

The importance of positive interactions has now been accepted and there are many attempts to integrate it into various general concepts to explain population, community and landscape level ecology. Bruno et al. (2003) have proposed a revision of the niche theory, positive density dependence at high population densities, relationship between species diversity and community invisibility and role of competitive dominants. The expansion of niche is based on the model proposed by Hacker and Gaines (1997), where the realized niche is expanded by facilitation, which is itself a modification of the intermediate disturbance hypothesis (Sousa 1979). This model can in fact explain increase in diversity by facilitation with increasing disturbance from medium to severe. Michalet et al. (2006) further developed these ideas, suggesting that facilitation promotes diversity at medium to high environmental severity by expanding the range of stress-intolerant competitive species into harsh physical conditions.
Since facilitation has been recognized as an important structuring force in natural plant communities, it is being recommended for developing vegetation restoration tools, particularly in severe and highly disturbed environments. Many ecosystem engineers/facilitators have significant effects on important ecosystem processes of management concern—hydrology, nutrient cycling and retention, erosion and sediment retention, for example—while at the same time creating habitat for other species that also influence biogeochemical processes via nutrient uptake, conversion, and release (van Breemen & Finzi 1998). ‘Finally, humans are often responsible for the loss or introduction of such engineering species, with the potential for large secondary consequences’ (Coleman & Williams 2002). So there is considerable potential for applying the ecosystem engineering concept in management. Ecosystem engineers can be important in controlling local microclimate and could therefore be influential in maintaining refuges for other species, even in the face of climate change (Cavieres et al. 2002). There are many studies reporting strong facilitative effects during restoration in high mountain environments (Aerts et al. 2007), and Mediterranean regions (Gómez-Aparicio et al. 2004) and tropical rain-forests (Parrotta et al. 1997).

Identifying the facilitator or ecosystem engineer that are of disproportionately important, so that it can be managed to assist in proactive management is necessary (Hobbs et al. 2006). But predicting apriori which species will be important as physical engineers is difficult (Jones et al. 1997). Research and management should be guided by strategically
identifying key knowledge gaps, and use precious and little available resources to maintain single species that could ensure ecosystem conservation (Brooker et al. 2008).

Most of the studies regarding plant–plant positive interactions, focus on ‘nurse plant’ benefits found in conditions of high stress. These nurse plants, create ‘islands of fertility’ (Schlesinger & Pilmanis 1998; Aguiar & Sala 1999), found either in patches or bands leading to so-called tiger or leopard vegetation (Aguiar & Sala 1999) reflecting the redistribution of resources and propagules. These patches of vegetation have been the focus of study for a long time (Kershaw & Looney 1985), including the role of nurse plants (Shreve 1931).

Nurse-plants are have recorded in deserts (Suzan et al. 1996), alpine regions (Cavieres 2006), salt marshes (Bertness & Yeh 1994), inter-tidal regions (Bertness & Leonard 1997; Stachowicz 2001; Bruno 2001), Mediterranean regions (Gómez-Aparicio et al. 2004) Many studies have found that the species richness under or around these nurse plants is significantly higher than that found in bare areas. There are even reports of them facilitating invasives in Andes (Cavieres 2008).

Successful recruitment is crucial for the establishment and maintenance of population levels of any species (Bertness & Yeh 1994), and nurse plants provide optimum conditions for germination, seedling emergence and establishment by creating spatial heterogeneity in an otherwise harsh environment. In any given case the collection of
factors or any single of these factors that make nurse plants, facilitators can differ (Stachowicz 2000; Bruno 2001; Gómez-Aparicio et al. 2005a, 2005b).

The shade of the nurse plants regulates the soil temperature and the ambient temperature and by reducing evaporation of soil moisture makes more water available to young plants (Shreve 1931; Holmgren 1997). In addition the evapotranspiration of the plant are less under shade (Franco-Nobel 1989). Soil temperature is very important to determine the health and growth of the newly germinated radicle, which can dry fast. Holmgren (1997) found that there is an interaction of micro-climatic gradients and physiological tradeoffs, so in mesic conditions where shade is the detrimental factor, as water is available everywhere in the environment. But in xeric conditions marked by extreme temperature (high in case of arid regions) and low moisture, life in the high light conditions is nearly impossible, so the plants survive better under shade.

Many studies have found that the photosynthetically active radiation is better suited to plant germination under shade than in bare areas (Valiente et al. 1991; Casal et al. 2001). The higher organic matter content under the shade of nurse plants occurs due to abiotic processes, mainly driven by wind and water, include redistribution of fine soil particles, associated mineral nutrients and litter that is concentrated underneath vegetated patches. Biotic processes results from the action of roots, which absorb nutrients from the soil under the densely vegetated patches, as well as from the soil of the bare-soil matrix (Aguiar & Sala 1999). The vegetated patches also manage to accumulate more propagules due abiotic factors like wind and rain and by biotically by attracting seed
dispersers like animals and birds by providing perches for them or because they bear fruits. (Aguar & Sala 1999).

Besides interactions, vegetation climax, is one of the most important concepts in succession. The existence of a single endpoint the climax vegetation by Clements (1914), for a given set of climatic characteristics of a site, has been recurrently challenged, being replaced by the acceptance of poly-climax based on differences in habitats giving edaphic, topographic, fire, and zootic climax (Singh et al. 2006). Absolute climax has been considered an abstract concept since communities are repeatedly subject to disturbances that prevent a community from being at equilibrium (Sheil 1999). Yet the concept of a single climax has endured criticism, and is tacitly accepted in research (Pickett 1976). In fact, most studies evaluate the rate of succession, based on the comparison of sites with the 'climax primary forest' as the possible endpoint, either in terms of species composition or structure of forests in degraded tropical environments (Corlett 1989; Myster & Walker 1997; Zhuang & Corlett 1997; Sheil 1999; Rivera et al. 2000; Lu et al. 2003; Kobayashi 2004; Lebrila-Trejos et al. 2008). Determining the resilience of different forest types and the recovery time needed for any landscape to resemble the possible climax, is a dominating theme in recent successional studies.

Ewel (1980) found that tropical dry forest (TDF) succession had few seral stages, so predicted more resilience, compared to humid tropics. Though there is increasing convergence through time, the rate of succession decreases in time (Myster 1984; Myster & Pickett 1990). Resilience is influenced by the habitat type and the initial conditions of
the site including the type of disturbance (Keever 1983; Myster & Pickett 1990, 1992). Degraded lands need more time for recovery (Uhl et al. 1988; Lugo 2002). The resilience rates recorded in TDF have been also influenced by methodological constraints like the choice of reference sites, and sampling criteria used (Kennard 2002; Pena-Claros 2003; Lebrija-Trejos et al. 2008).

The TDF succession is characterised by a short early phase dominated by herbs and shrubs, followed by a pioneer tree phase to be replaced by primary forest species (Lebrija-Trejos et al. 2008). They also found that dominant pioneer species were absent from the natural regeneration dynamics of the mature forest, which is in contrast with most secondary successions in TRF, where species that colonize fallows are generally the same ones involved in the gap dynamics in mature forest.

Grasses and herbs dominate for two years in Mexico and for eight years in Bolivia (Kennard 2002). There was a recovery of species richness, with maximum reached at mid-successional stages, but not the original composition (Aide 1996; Colon & Lugo 2006; Lebrija-Trejos et al. 2008). Aide et al. (1996) found species diversity low till 10 years, then began increasing from 10-15 years to 40 years in Puerto Rico. In another also in Puerto Rico in 45 years species level were similar to than in the forest (Colon & Lugo 2006). In Bolivia, Pena-Claro (2003), and Toledo and Salick (2006) found that the species richness was higher in the under storey, than in the upper storey.
The convergence of vegetation structure was faster. Aide et al. (1996) found density, basal area and height were similar to the forest in 40 years, as did (Lebrija-Trejos et al. 2008) while it reached 70 % in the a Bolivian forest by 25 years and 50 years (Pena-Claros 2003) and kept increasing with age in others (Toledo & Salick 2006). Density for trees peaked after 25 years to 14,000 trees/ha in Puerto Rico for trees ≥ 1 cm dbh. Density of trees exceeded and was twice as much as forest density in Bolivia (Kennard 2002)

Basal area increased from 5m²/ha in 9.5 years to 40m²/ha for trees ≥ 1 cm dbh in 60 years in Puerto Rico (Aide et al.1996); and from 12.3 m²/ha in the 2nd year to 36.3m²/ha for trees ≥ 1 cm dbh in 40 years (Pena-Claros 2003) and 2.9 m²/ha in 5 years to 21.6 m²/ha in Bolivia (Toledo & Salick 2006). Basal area was the attribute that showed the slowest recovery in Mexico (Lebrija-Trejos et al. 2008).

The distribution of size-class of trees ≥ 10 cm, showed maximum density in lower size classes < 20 cm dbh (Kennard 2002) and Ruiz et al. (2005) found that 61% of the trees with dbh (2.5 to 5 cm) and 35 % with height (>2.5-5 m). They found a reverse J-shaped population structure as did Sabagol (1992) in Nicaragua with 87% of trees < 30 cm dbh and average height of 15-30 m. In Bolivia, Kennard (2002) found cover was limited to 10-20% in 1,2,3 years but increased to 56% in 5 years.

Seed dispersal is one of the important limiting factors in recruitment of species. In dry forests wind is the most common mode of dispersal (Bullock 1995). In the TDEF area, where the study was conducted, endo-zoochory (69.2%) and anemochory 14% are the
most important dispersal mode (Swamynathan & Parthasarathy 2005). The mode of dispersal can differ with habitat type, with presence of perches or forest edges enhancing zoochory (Janzen 1988; Parrotta 1995). In Amazonia, autochory (60%) was the dominant dispersal mode in open herbaceous areas with anemochory (40.2%) and endo-zoochory (37.8%) being dominant in forest shrub vegetation (Arbelaez & Parrado-Rosselli 2005).

Besides primary dispersal agents like wind, water, gravity and animals, secondary dispersal by another agent from the first landing site of a dispersed seed can occur. Ants have been known to remove tiny seeds from animal droppings or from under the parent tree to their nests (Turner 2001). Endochory can occur passively when the fruit is eaten as part of a larger vegetation part by herbivores (Elcott et al. 2007) or actively when animals eat the fruit for the reward offered by the plant. It is sometimes an expendable fleshy part, in which case the seed is dispersed after passing through the gut or mouth of the animal or the seed itself, where the seeds are hoarded and forgotten by animals (Turner 2001).

Though endochory is important, the importance of different herbivores is unclear. Elcott et al. (2007) found that endochory is an important agent of local and regional population dispersal and support persistence via metapopulations. Since large herbivores can travel far they can disperse seeds further than small mammals and are particularly important in successional matrix having profound effect on community development and structure. (Elcott et al. 2007).

With the exception of a few pantropical weed trees, the woody successional flora of each major tropical area- Africa, Asia, and Americas is restricted to that area, though there are ecological equivalents (Ewel 1980). Kellman (1980) predicted a homogenous herbaceous
weed flora and nucleated succession dominated by secondary trees species in recovering forests. Most of the flora of earlier seres were reported from successional studies around the world.

Given the sub-continent that India is, Champion and Seth (1968) have listed 37 forest types based on Thornthwaite’s 1948 climatic types, while they have themselves identified 162 vegetation types based on a mixture of factors like climate, edaphic, other site factors, and biotic influences. These forests are inclusive of sub-groups based on degradation due to human resource use and identifiable seral stages of the vegetation and are listed below:

Table 1: Forest types are groups and sub-groups classified under different biomes in India.

<table>
<thead>
<tr>
<th>Biomes</th>
<th>No of Forest types</th>
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<tbody>
<tr>
<td>Moist Tropical forests</td>
<td>62</td>
</tr>
<tr>
<td>Dry Tropical forests</td>
<td>39</td>
</tr>
<tr>
<td>Dry Montane Subtropical forests</td>
<td>17</td>
</tr>
<tr>
<td>Montane Temperate forests</td>
<td>31</td>
</tr>
<tr>
<td>Sub-Alpine forests</td>
<td>6</td>
</tr>
<tr>
<td>Alpine scrub</td>
<td>7</td>
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There have been relatively few studies on secondary succession, in India, compared to the vast diversity of forest types seen. Most of these studies have focused on the moist forests prevailing in Western Ghats (George et al.1991; Pascal 1988) or northwestern India (Rao & Ramakrishnan, 1987) A previous study of succession in the tropical dry evergreen forests (TDEF) in North Arcot and South Arcot areas recorded eight successional stages leading from the *Aristida* spp. dominated grass stage to the climax constituted by *Albizia amara- Acacia leucophloea* communities (Dabholkar 1962)

Degraded lands in India are considered as being seral in nature, having originated due to abandoned cultivation or degradation of forests, resulting in grasslands and considered as disclimax (Misra 1959). Though there are few studies to document the effect of grazing on species interactions, there are many studies that have been conducted in grasslands to evaluate the effect of grazing on species diversity, biomass productivity. A pattern of increase in species diversity and net productivity of grasslands due to moderate levels of grazing and loss of species under heavy grazing regimes is reported from Himachal Pradesh, Varanasi and tropical savannas in India (Singh & Mishra 1969; Swartzan & Singh 1974; Pandey & Singh 1992, Saberwal 1996), and from Serengeti in Africa (Mc Naughton, 1979, 1993; Belsky 1992) to British limestone grasslands (Gibson & Brown 1992). However, continued grazing can increase not only recruitment but also extinction (Gibson & Brown 1992).

Studies comparing grazed intensities, found that there was decrease in palatable species, up to 30 % and increased the dominance of only a few species in Sahel, Africa (Heirmaux 1998). Studying vegetational composition at increasing distance from a water
source Sasaki et al. (2008) found that the influence of grazing was more on volume than on composition.

Heavy grazing selectively favours the establishment of short turf and creeping perennial such as *Allopterus cimicina*, *Bracharia distachya*, *Digitaria longifolia* in Sri Lanka, and thorny species of *Acacia*, *Prosopis* and *Zizyphus* in the Vindhya. Grasses like *Bothrichloa pertusa*, *Desmostachya* sp, *Digitaria* sp occur with leguminous weeds like *Cassia tora*. As a result of protection from fire and grazing, in 16 years there was an increase in tree species richness from 4 to 16 and the tree density increased from 14.6- and 3.7-fold (Jose-Fraimias 1983).

Sometimes it is the herbaceous flora of the early seres that is socially and economically important and maintained by grazing as in the famous Valley of flowers in Bhuynder valley in the Nanda Devi National Park in Himalayas. An ever increasing list of endangered species promoted the Indian government to impose a total ban on grazing in 1982. A study conducted by Nathani et al. (1992) showed that there is subsequently less mineralization of soil nutrients and the natural course of succession has helped the establishment of a few successional woody species, which would eventually lead to the elimination of the herbaceous species.

Previous studies on the early to middle stages of succession have shown that grazing can reduce grass cover and favour establishment of woody plants, by reducing competition from grasses and risk of fires, and improving dispersal of seeds of woody species by grazing animals (Van Auken 2000; Roques et al. 2001).
Specialization of tropical plants for habitat and micro-habitats, has been used to explain their co-existence and the high species diversity in tropical forests (Denslow 1987; Gentry 1988; Clark et al. 1995) and savannahs (Barot et al. 1999), with the species regarded as being segregated along various environmental niches like light, soil moisture and nutrients (Silvertown 2004). Mass-effects, whereby the species establish in sites through input of propagules from nearby favourable habitats in the absence of self-sustaining populations is also important in explaining species richness (Shmida & Wilson 1988).

Microhabitat refers to environmental conditions that vary at scales less than 10^3 metres, and habitats refer to strong environmental discontinuity, usually at larger scales according to Svenning (1999). Regeneration niche is regarded as the most important niche, as plants' sensitivity to factors changes with age and they are most vulnerable when they are young (Collins & Good 1986; Svenning & Balslev 1999). There have therefore being many studies that study regeneration niche's importance to explain spatial patterns, and their influence on density and population structure.

Collins and Good (1986) compared the habitats of six tree species to consider their effects on the regeneration of species and found factors like light, litter depth and nearest neighbour occurrence as important. Various other factors have been known to influence plants, including palms. The distribution of palms too, across tropics provide evidence of the influence of heterogeneity at the level of habitats (Kahn & De Castro 1985; Peres 1994), and microhabitat as seen in the Amazonian palm community (Svenning 1999),
Costa Rican palms (Clark et al. 1995) and African *Borassus aethiopum* (Barot et al. 1999).

Clark et al. (1999) found that the distribution of palms at a scale of <1 km² were influenced by topography and edaphic factors. Clark et al. (1995) found twice the density of palms on the steep slopes compared to gentle or lower slopes, with spatial heterogeneity at small to large scales (0.5 to 10 m²) affecting community structure. Similarly Svenning (2001), found six species of palms in the Andean forests to be correlated with altitude and aspect of mountains as well as edaphic factors.

Schwaegerle & Bazzaz (1987) studying nine populations of Phlox in Texas, along environmental gradients of several factors like light, nutrients, competition found that populations of large plants were less sensitive to change availability than smaller plants. Differentiation in populations occurred due to many processes, and populations in closed habitats are genetically different from those in open habitats, allocating more resources to persistence and competition and less to production of propagules for dispersal (Schwaegerle & Bazzaz 1987).

There is evidence that there is heterogeneity in microsites in homogeneous habitats (Collins & Good 1986; Palm & Dixon 1990). Resource availability like soil, moisture, light and nitrogen varied within patches of uniform vegetation and the range of resource spatial difference was different among resources within a single community type. This
heterogeneity in resource distribution is reflected in the distribution of plants (Collins & Good 1986; Dunslow 1987).

The difference in distribution begins with arrival of propagules. In heterogeneous environments seeds settle in some sites more readily than in other sites irrespective of whether these sites are favourable for germination, growth and establishment of the species (Bernard & Toft 2008). Pioneers were found to regenerate better in lighter microsites and primary forest species in darker microsites (Clark et al. 1993).

Besides regeneration, environmental factors influence other stages of plant life too, like growth and phenology. Light was found to be an important factor for growth and reproduction, leading to population level consequences. (Oyama 1990; Svenning 2002). In 11 populations of the dioecious herb Jack-in-the-pulpit, *Arisaema triphyllum* (Araceae), studied for two years, Doust and Cavers (1982) found that the allocation of resources differed among the genders depending on the type of habitats they were found in. Female plants were found in microsites that had more light, soil pH and nutrients and male plants were found in microsites that had less light, soil pH and nutrients. The size of plants also differed, females being 3.5 heavier than males, and allocating twice as much of dry matter to flowers than males. More male flowers/plants in harsh habitats and more of female flowers/plants in favorable environments have been reported in dioecious *Calophyllum brasiliense* (Fischer & Dos Santos 2001) and in the Egyptian *Thymelaeas hirsuta* (Ramadan et al. 1994). Clark et al. (1987) found that in Zamia *skinneri*, a long lived dioecious cycad, that light and plant size affected reproductive effort, with three
episodes of flowering in the secondary forest and only two in the darker primary forest in a period of six years.

In dioecious plants, various environmental gradients like nutrients (Cox 1981), temperature and soil moisture content (Freeman et al. 1980; Freeman & Vitale 1985), and light (Onyekwelu & Harper, 1979), along which sexes segregate have been identified producing deviations of sex ratio from 1:1 (Meagher, 1980). A male-biased sex ratio is usually more common in dioecious plants, as found in Chamaelirium luteum a lily (Meagher, 1981), Borassus aethiopum a savannah palm (Barot et al. 1999), double coconut (Savage & Ashton 1983; Silvertown 1987), and the cycad Zamia skinneri (Clark & Clark 1987).

Among all factors light emerges as the single most important factor that affects distribution, density and population structure. Tree species can in fact be arranged along a continuum of adaptive response to the availability and duration of incident radiation (Denslow 1987). Light is necessary for regeneration, establishment and growth of seedlings (Denslow 1987; Clark et al. 1987, 1993; Svenning 2002), for growth of the plant and reproductive activity (Oyama 1990; Chazdon 1986; Svenning 2002).

The differential needs of resources and therefore choice of habitats and microhabitats by plants is one of the major driving force that can explain the density, dispersion and population structure of species (Alvarez-Buylla 1994; Barot et al. 1999). The reverse J structure that populations usually show, though, is more a consequence of density
dependant mortality in the youngest ontogeny, than spatial heterogeneity (Van Valen 1975; Pinard 1993; Silva Matos et al. 1999; Souza & Martin 2002). In some palms the seedlings were found with adults as in *Iriartea deltoidea* (Svenning & Balslev 1999) but many studies also report seedlings being found away from the parents in palms such as the Brazilian acaulescent palm *Attalea humilis* (Souza & Martin 2002), and *Euterpe edulis* (Silva Matos & Watkinson 1998) The influence of spatial heterogeneity influences all the ontogenic stages, as demonstrated in *Attalea humilis* (Souza & Martin 2002), where fire was the influencing factor, while Barot et al (1999) found that the clumped dispersion of all the ontogenic stages in the African *Borassus aethiopum* was due to nutrient rich patches in a savannah.

There are however relatively few ecological studies of palms, with most studies dealing with taxonomic or economic botany of the family (Borchsenius et al. 1998) even though Arecaceae is one of the most useful group of plants distributed in the tropics and parts of subtropics, consisting of 201 genera and 2650 species (Mabberley 2000). Palms are economically important as they include major plantation species like oil palm, coconut and date palm. However, most palm products are non-commercial, being part and parcel of daily life in rural areas worldwide, used predominantly for food, thatch, handicrafts, construction and medicine (Basu & Chakravarty 1994; Borchsenius et al. 1998).

Most of the degraded lands or ‘wastelands’, as they are commonly called, serve as common property resources (CPR) In India, owing to their degradation, they do not offer high returns to their users, hence only the rural poor and intermediary households use them for fodder and fuel wood. Such ‘wastelands’ contribute to employment, asset
accumulation and to 14–23 per cent of the income, especially for the rural poor (Jodha 1989). Patterns of use vary with gender, with the women being recorded as the predominant resource users in Himachal Pradesh (Berkes et al.1998).

‘Wastelands’ in India are estimated at 6385 million hectares, accounting for 20.17% of the total land area (328.73 million hectares), according to the National Wastelands Inventory Project, undertaken by National Remote Sensing Agency (2000). There are 13 categories of wastelands, of which degraded forests makeup 4.44% and grazing lands 0.82%, degraded land under plantation 0.18%, land with or without scrub 6.13%, gullied and ravenous land 0.65% of the total Indian land mass. Of the total designed wastelands, 50% are non-forest areas.

The land ownership is private fallow land, village/Revenue land or forests. The negative image of the ‘wastelands’ has ensured that it has long been a target for various development schemes by the Central and State governments. The nation wide Social forestry programme instead of supplying fodder and fuel for the local people was diverted for commercial and industrial use (Singh 1985). The Comprehensive Wasteland Development Project in Tamil Nadu initiated in 2002–2003 seeks to lease a hundred thousand hectares of community lands to corporates, besides private wastelands, without listing benefits for the local people (Sarvanan & Mahapatra 2003). Among the latest threat to the local population’s access to ‘wastelands’ for usufruct benefits is the proposal to use 11 million hectares of ‘wastelands’ (7 per cent of the cultivable area in the country) for monocultures of Jatropha by 2012 to supply biofuels, to meet India’s aim to achieve 20 per cent blend of bio-diesel by 2010 (Mishra & Awasthi 2006). The long-term
requirement to keep carbon in storage in forestry projects required to be maintained for
Clean Development Mechanism (CAD) under the Kyoto Protocol to mitigate climate
change, if implemented in India, can also conflict with the short-term needs of the poor, if
the energy and other biomass needs from the CPR are not addressed and the benefits of
carbon sequestration is not channelled to the rural poor, leading to tensions and erosion of
benefits (Gundimeda 2004).

So it is necessary to incorporate social science research with ecological research for
successful landscape restoration (Sabagol 1992, Sanchez-Azofeifa et al. 2005) Parch et
al. (2001) recommend using spontaneous succession for ecological restoration, a
relatively new field, keeping in mind the aims of project restoration of climax vs
reclamation for socially acceptable condition or productive use, and evaluation of site
environmental conditions before deciding whether spontaneous succession is an
appropriate way to achieve the aims. This should be supported by predicting successional
development, suggesting possible intervention (cultural practices or species introduction)
at appropriate junctures of succession and monitoring of results.

There are mixed reports of the effect of different kinds of management. The choice of an
appropriate overstorey species in plantation is critical as the one 'catalyze' succession by
influencing subsequent patterns of colonization. Nineteen species of secondary tree
species were found established under Casuarina equisetifolia, Eucalyptus robusta and
Leucaena leucocephala, while there was no regeneration in bare unplanted areas (Parotta
1998). George et al. (1991) too found that after 15 years the understorey in a Eucalyptus
plantation in the Western Ghats, near wet evergreen forest had reached species richness
levels similar to the forest. However, exotics are generally considered less suitable for reforestation projects as they can turn invasive, so the search for suitable local species is important (Blanc et al. 2002). Restoration projects that skip early successional species and plant only late successional species have less understory richness (Aide et al. 1996). The use of shrubs as nurse plants facilitating later successional species has been advocated for the Mediterranean regions (Castro et al. 2002; Gomez et al. 2004, 2005). A recent study shows that rotating grazing land to reduce grazing pressure in dry forest pastures in Nicaragua, recorded a total of 85 forest species found as adults in the pastures, of which 60 and 30 species were able to establish as seedlings and saplings (Esquivel et al. 2008) So spontaneous succession, with a little intervention can help in conservation of tree species in the predominantly agricultural landscapes in tropics.

Rehabilitation of degraded tropical landscapes by identifying stress-tolerant, native or exotic species and appropriate management systems has made significant contributions. Since wood and non-wood products are both important 'the focus of "wastelands" reforestation programmes for fuelwood/timber should be broadened to rehabilitation forestry' (Parotta 1998).

It is possible to speed up designing appropriate resource management programs, by incorporating traditional ecological knowledge (TEK), based on local people's understanding of ecological processes (Berkes et al. 2000). There has been a growing interest in TEK since 1980s to study species identification and classification eg. enumeration of 48 species of mushrooms in Mexico (Montaya et al. 2003), study and
proceeded to people understanding of the ecological processes (Alcorn 1989; Gadgil 1993; Huntington 2000).

Local communities have been known to use their TEK to manage ecosystems and respond to changes showing a understanding of the complex processes at work in nature (Berkes et al. 2000) TEK has been useful in saving species biodiversity (Gadgil 1993), rare species, recognizing and protecting keystone species and to protect habitats (Johannes 1998; Berkes et al. 2000). In India, sacred grooves are an example of habitats protected by cultural beliefs. (Gadgil 1993; Parthasarathy et al. 2008).

But while there are many promoters of TEK, there have been very few cases of synthesis of TEK and science. Many promoters have themselves cautioned against unquestioned use of TEK (Huntington 2000), since it can be wrong as these are knowledge systems that are usually shared and passed on orally. There is also inertia to embrace this new interdisciplinary approach to research, but which, could be overcome by evidence from studies documenting and incorporating TEK. Many are reluctant and unwilling, to use TEK considering it lacking in scientific vigour; and to overcome the obstacle of using social science methods to document TEK and the reluctance of the TEK holders to share their knowledge (Huntington 2000; Berkes et al. 2000).

There have only a few instances when scientists and TEK holders have worked together, a whaling census being one (Huntington 2000). The Alaska Eskimo Whaling Commission, fought against the ban on harvesting bowhead whales in 1977 by the International Whaling Commission. They were allowed a harvesting quota based on the
census of whales. The original census of 2000-3000 whales based on visual observation was revised by considering visual and acoustic evidences from locations not considered earlier to increase the census figures to 6000-8000, based on information from Alaskan Eskimos.

But there are successful cases of management practices that have been based on local traditional knowledge and cultural practices, including preservation of remanant forest pat hes of the TDEF in sacred groves (Parthasarathy et al. 2008). Jhum or shifting cultivation was judged to be harmful in a biodiversity hotspot in northeastern areas of Himalayan leading to a regulation of shifting cultivation in 1947 and promotion of agroforestry as the a more suitable and economically sustainable. But there is realization now that jhum based on years of practice and refinements, involving use of local cultivars in fact is better for conservation of biodiversity and soil and there are now efforts to promote it again (Arunachalam et al. 2002).

Since the last twenty years many countries have handed over management of natural resources to the local communities, which have to be monitored. When management plans and monitoring systems are participatory, incorporating TEK along 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).

The Irulas are a hunter-gatherer tribe inhabiting parts on the Coromandel coast since pre-Dravidian times, whose TEK has been tested and used several times in conservation of
biodiversity and restoration. Their skills as hunters has been used in modern medicine, to collect venom of snakes used in producing anti-venom for bites of the four most poisonous snakes in India and their knowledge of forest plants and their medicinal value has been documented and their herbal medicines are being marketed (Methil 2008, Madras Crocodile Bank 2008).