

Ecology of seed and seedling growth for conservation and restoration of tropical dry forest : a review

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Summary

Dry forests are among the most threatened ecosystems and have been extensively converted into grasslands, secondary forest, savanna or agricultural land. Knowledge of seed germination and seedling establishment is required for the success of efforts on restoration of these forests. This review focuses on the ecological requirements at seed and seedling stages, and collates the current knowledge of seed viability, dormancy, germination pattern and seedling behaviour of dry tropical tree species. The spatio-temporal variations within the tropical dry forest biome in soil moisture, light, temperature, nutrients and intensity of predation, significantly affect the seed and seedling traits of component species. The majority of dry tropical species possess orthodox seeds which are characterized by dormancy, while a few have recalcitrant seeds which possess little or no dormancy. Seed coat dormancy, which can be overcome by mechanical or acid scarification or sometimes by transit through animal guts, is most prevalent in the dry tropical forest species. Persistent species dominating the undisturbed portions of the forest have bigger seeds compared to those that mostly occur in disturbed regions and require shade for the survival of their seedlings. Shade demand is associated with drought endurance, and may be absolute in species such as *Guettarda parviflora* and *Coccoloba microstachya*, or facultative as in *Plumeria alba* and *Bursera simaruba*. The fluctuation in temperature significantly affects seed germination in several species of dry Afrotropical forest trees of Ethiopia. Seedling mortality is primarily a function of moisture stress during the dry period. Adaptive responses of seedlings to drought stress include increased chlorophyll content, for example in *Acacia catechu*, and root biomass, as in several dry forest species (for example *Drypetes parvifolia*, *Teclia verdoornia*) of Ghana. Mulching, application of fertilizers, interplanting of leguminous species and mycorrhizal inoculation are useful tools for promoting seedling establishment in

nutrient-poor dry tropical soils. Periodic forest fires, and predation affect recruitment and seedling development according to their intensity. Many species experiencing frequent fires have evolved thick seed coats, produce fire-hardy seedlings, or escape the effect by temporal separation of seed dispersal and fire events. Predation may result in abortion of fruits or may enhance germination and recruitment by scarification and dispersal, as in most species of the Guanacaste dry forest. Exposure to elevated CO₂ has increased relative growth rate, total leaf area and water use efficiency in most of the dry tropical seedlings tested, but the magnitude of the effect has varied markedly among species. Due to the availability of a large source of energy, large seeds show higher germination percentage, greater seedling survival and increased growth. Seeds originating from different provenances exhibit differences in germination and seedling growth (for example *Prosopis cineraria*, *Albizia lebbek*, *Eucalyptus camaldulensis* and *Acacia mangium*), efficiency of nodulation (for example *Acacia nilotica*, *A. auriculiformis*), and stress resistance (for example *Populus deltoides*, *Dalbergia sissoo*). The review points out the need for coordinated, long-term, field-based studies for identification of multiple cues and niches for germination, on seed and seedling dynamics in response to fire, and on within-species genetic variability for selection of suitable provenances. Field-based studies at species and community levels are also needed to permit manipulations of biotic components to augment the recruitment of desired species and to suppress that of undesirable species.

Keywords: mycorrhiza, seed dormancy, seed size, seed viability, shade demand, restoration

Introduction

Tropical dry forest constitutes tree communities growing in warm to hot climates with a pronounced seasonality in rainfall and 2–6 months of drought each year during which the ratio of potential evaporation to rainfall (E/R) is greater than one (Olivares & Medina 1992). These forests occur over large areas in Central and South America, Africa, India, South-

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East Asia and Australia (Gerhardt & Hytteborn 1992). The pronounced seasonality affects the patterns of seed production, germination, survival and seedling development. The favourable growth period in the dry tropics is usually restricted to the short rainy season when seeds are expected to germinate and seedlings established. The canopy of dry forest is renovated in the pre-monsoon period (Singh & Singh 1992), and therefore seedlings emerging in the rainy season experience reduced intensity and modified quality of light under relatively closed canopies, and those in the open encounter high light intensity and face competition from fast-growing dense populations of herbs. Thus emergence, establishment and growth of seedlings face very heterogeneous situations in dry forest as compared to rain forest.

Dry forests are more threatened and less protected than moist and wet forest (Gerhardt 1993). Also, the original extent of dry forest will never be known, since many of them were converted into grasslands, open secondary forest, savanna, or logged, burned and converted into cattle ranches or agricultural land over hundreds of years (Murphy & Lugo 1986; Swaine 1992). In Central America, only <2% of tropical dry forest have remained in a more or less intact state and <0.1% have some kind of conservation status (Janzen 1988a; Sabagal 1992). The status of dry forest is just as critical, or worse for regions of Australia, south-east Asia, Africa and major parts of South America (Janzen 1988a). Dry forest is now frequently a mosaic of disturbed open-canopied, and relatively undisturbed close-canopied patches at several spatial scales which constitute a marked heterogeneity in terms of irradiation, temperature, moisture and rate of nutrient release from decomposing litter. The conversion of tropical forests into land for agriculture is a major threat to biodiversity (Dobson *et al.* 1997). Large areas need to be brought back under forest cover in order to reverse the current trend of deforestation and to conserve biodiversity. The natural colonization and successional process, however, may go in an undesired direction, as the species that arrive first by chance may persist and dominate the ecosystem for a long period of time leading to a further loss of biodiversity. Human interference may therefore be necessary for careful manipulation of initial composition of species to get the desired end-product of restoration (Dobson *et al.* 1997). The successional process can be accelerated by introducing desired species through seeding, moving intact seed banks, and planting seedlings (Skoglund 1992).

Aspects of seed ecology such as soil seed banks and their role in succession, adaptive value of large seeds and patterns of seed longevity and germination have been reviewed for tropical rain forest species (see for example Whitmore 1983; Foster 1986; Vázquez-Yanes & Orozco-Segovia 1993). However, the scattered information on seed and seedling ecology of dry tropical forest species has not been reviewed previously. We believe that knowledge of seed germination and seedling establishment is not only important for understanding the community processes such as plant recruitment and succession, but is also required for the success of efforts

on augmentation, introduction, and re-introduction of species populations in restoration efforts. The information on the ecological requirements at seed and seedling stages is seldom articulated in forest conservation and management plans.

This review collates the current knowledge of seed viability, dormancy, germination pattern, and seedling behaviour of dry tropical tree species. Soil moisture, temperature and fire, light, soil nutrients, predators and parasites are recognized as major environmental factors influencing seedling recruitment in these forests. Roles of mycorrhiza, elevated CO₂ and inter- and intra-specific differences in seed size and seedling establishment and growth are also reviewed. We recognize that populations of a species growing in different environments may show differential germination and seedling growth efficiencies and therefore a consideration of seed provenances is essential for a successful restoration effort. Although a substantial amount of illustrative material is drawn from India, it is hoped that the synthesis will be of use in restoration efforts throughout the dry tropical forest region.

Seed viability and dormancy

Dry tropical forest trees produce both orthodox and recalcitrant seeds. Orthodox seeds, such as those of *Acacia nilotica* and *Gmelina arborea*, can be stored at low temperatures for a longer duration without loss of viability. Many dry forest tree seeds, however, lose viability quickly under ordinary conditions and sometimes even in cool dry storage condition (Ray & Brown 1995). Seeds of *Shorea robusta*, which are common in both moist and dry tropical forests, remain viable for only 7–10 days (Saha *et al.* 1992). This short viability is due to a very high rate of moisture loss which is associated with loss of hair from the seed coat. Increased leachate conductivity and decreased fatty acid content due to ageing in certain seeds (for example *Dalbergia sissoo*) are other reasons for loss of viability and decline in germination percentage (Thapliyal & Connor 1997). Seeds of certain dry Afromontane forest species of Ethiopia, such as *Bersama abyssinica*, *Myrsine africana* and *Pittosporum viridiflorum* were recalcitrant, while those of *Ekebergia capensis* showed a decline in germination with increasing time of storage (Teketay & Granstrom 1997).

The proportion of viable seeds might depend on the time of seed collection. For example, collection of seeds of *Dalbergia sissoo* during the period November to July, yielded maximum numbers of viable seeds (Bangarwa *et al.* 1996). Temperature conditions and kinds of storage container found best for retaining maximum seed viability are known in certain Indian dry tropical species (Table 1). It is evident that a considerable amount of diversity exists with respect to optimal storage temperature. While a number of species such as *Albizia lebeck* and *A. procera* need low temperatures (3–5°C), others, including *Azadirachta indica* and *Dalbergia sissoo*, require higher temperatures (15–25°C), and still others can withstand much wider ranges (Table 1).

Table 1 Reported optimal temperature and storage container to maintain maximum seed viability of certain dry tropical species. For most species optimal moisture content was 7–8%.

Optimal temperature (°C)	Species	Storage container	Source
3–5	<i>Albizia lebeck</i>	Paper packet	Babley (1985)
	<i>Albizia procera</i>	Glass stoppered transparent bottle	Kandya (1990)
	<i>Bauhinia variegata</i>	Paper packet	Babley (1985)
	<i>Cassia siamea</i>	Glass stoppered transparent bottle	Kandya (1990)
	<i>Ceiba pentandra</i>	Air tight polyethylene bags	Kandya (1990)
	<i>Dendrocalamus strictus</i>	Silica gel or anhydrous CaCl ₂ in desiccator	Gupta and Sood (1978)
	<i>Peltophorum ferrugineum</i>	Glass stoppered	Kandya (1990)
15	<i>Azadirachta indica</i>	Perforated polyethylene bags	Maithani <i>et al.</i> (1989)
	<i>Bambusa tulda</i>	Sealed polyethylene bags	Thapliyal <i>et al.</i> (1991)
	<i>Eucalyptus deglubta</i>	Closed container	Doran <i>et al.</i> (1987)
	<i>Eucalyptus microtheca</i>	Closed container	Doran <i>et al.</i> (1987)
	<i>Flinderria brayleyana</i>	Closed container	Doran <i>et al.</i> (1987)
20–25	<i>Dalbergia sissoo</i>	Tin	Ashwathanarayana <i>et al.</i> (1996)
	<i>Shorea robusta</i>	Non sealed polyethylene bags	Purohit <i>et al.</i> (1982)
	<i>Shorea talura</i>	Non sealed polyethylene bags	Purohit <i>et al.</i> (1982)
15–35	<i>Acacia auriculiformis</i>	Glass stoppered bottle	Kandya (1990)
	<i>Cassia glauca</i>	Air tight polyethylene bags	Kandya (1990)
30	<i>Holoptelia integrifolia</i>	Sealed container with silica gel	Maithani <i>et al.</i> (1987)

Table 2 Pretreatments yielding maximum germination in selected dry tropical species.

Dormancy type	Pretreatment showing best germination	Species (source)
Physical dormancy	Acid scarification	<i>Acacia auriculiformis</i> (Kandya 1990), <i>Acacia feruginea</i> (Thapliyal <i>et al.</i> 1998), <i>Acacia mellifera</i> (Jerlin & Vadivelu 1994), <i>Acacia nilotica</i> (Adeola & Dada 1986), <i>Acacia pseudo-eburnea</i> (Karihaloo 1984), <i>Acacia tortilis</i> (Karihaloo 1984), <i>Erythrina burana</i> (Teketay 1994), <i>Peltophorum ferrugineum</i> (Kandya 1990), <i>Terminalia bellirica</i> (Sharma <i>et al.</i> 1992)
	Hot water treatment	<i>Ceiba pentandra</i> (Kandya 1990), <i>Tamarindus indica</i> (Srimathi <i>et al.</i> 1990), <i>Prosopis juliflora</i> (Ashwathanarayana <i>et al.</i> 1996), <i>Dalbergia sissoo</i> (Ashwathanarayana <i>et al.</i> 1996), <i>Hardwickia binata</i> (Ashwathanarayana <i>et al.</i> 1996), <i>Erythrina brucei</i> (Teketay 1994), <i>Acacia catechu</i> (Karihaloo 1984), <i>Acacia decurrens</i> (Karihaloo 1984), <i>Acacia leucophloea</i> (Karihaloo 1984), <i>Albizia saman</i> (Srimathi <i>et al.</i> 1990), <i>Albizia odoratissima</i> (Ashwathanarayana <i>et al.</i> 1996), <i>Anogeissus latifolia</i> (Ashwathanarayana <i>et al.</i> 1996)
	Mechanical scarification	<i>Acacia farnesiana</i> (Thapliyal <i>et al.</i> 1998), <i>Acacia planifrons</i> (Thapliyal <i>et al.</i> 1998), <i>Albizia procera</i> (Kandya 1990), <i>Cassia glauca</i> (Kandya 1990), <i>Leucaena leucocephala</i> (Babley & Kandya 1985), <i>Olea europaea</i> ssp. <i>cuspidate</i> , <i>Acacia abyssinica</i> , <i>Podocarpus falcatus</i> , <i>Calpurnia aurea</i> , <i>Indigofera rothii</i> (Teketay & Granstrom 1997)
Physiological dormancy	Ca(OCl ₂) treatment	<i>Ailanthus excelsa</i> (Jacqueline <i>et al.</i> 1990)
	Thiourea treatment	<i>Albizia lebeck</i> (Roy 1992)
	KH ₂ PO ₄ treatment	<i>Azadirachta indica</i> (Kumaran <i>et al.</i> 1996)
	KNO ₃ or CaOCl ₂	<i>Casuarina equisetifolia</i> (Maideen <i>et al.</i> 1990)
	Exposure to gamma-rays	<i>Tectona grandis</i> (Duyasagar & Kothekar 1982)

The ability of a species to remain dormant is particularly associated with the seeds of species from unpredictable environments and climates with variable rainfall trends. In contrast to tropical rain forest species, of which about 62% produce non-dormant seeds, as many as 76% of dry tropical forest species produce dormant seeds (calculated from Baskin & Baskin 1998). Physical dormancy is most prevalent in dry tropical tree species and accounted for 67% of species producing dormant seeds, while only 23% showed suspected physiological dormancy. Per cent and rate of germination in

several species including *Acacia catechu*, *Albizia lebeck*, *Bauhinia variegata* and *Cassia fistula* increased when embryos were decoated (Babley & Kandya 1986). Many pretreatments have been successfully used to break dormancy (Table 2). Although acid, hot water and mechanical scarification have been found suitable in a majority of species, there are a few, such as *Olea europaea* and *Podocarpus falcatus*, which respond only to mechanical scarification (Teketay & Granstrom 1997).

Dormant seeds suppress the negative demographic effect of reproductive failure and permit the species to avoid

environmental conditions potentially unfavourable for seedling establishment. A hard seed coat allows endozooic dispersal (Teketay 1997). Also, seed coat dormancy prevents the seed from germinating during isolated showers in the middle of a long dry season while permitting it during a sustained rainy season (Willan 1985). Dormant seeds generally remain viable for long periods of time. The extent of dormancy even varies within a species, and as a result, individual seeds become permeable to water at different times which results in staggered seedling recruitment providing an insurance against spells of unfavourable conditions. The soil seed bank thus may produce seedlings continuously for several years due to different periods of dormancy. Passage through a digestive tract may enhance seed germination in various dry tropical species, for example, *Acacia constricta* (Cox *et al.* 1993), *A. cyclops* (Gill 1985), *A. nilotica* (Miller 1995) and *A. tortilis* (Miller 1995). Also, seeds of *Leucaena leucocephala* germinated to about 90% after a 240 h residence in rumen of cattle (Gardener *et al.* 1993). *Ficus benghalensis* showed higher germination of freshly-matured seeds when passed through the digestive system of a bird (Midya & Brahmachary 1991).

Seed size

Seed size is known to affect various aspects of plant life (Milberg & Lamont 1997); it influences the dispersal and seed water relations, and emergence, establishment, survival and growth of seedlings. Small seeds have a better chance to enter into the soil easily than large seeds, and thus, facilitate the build up of persistent soil seed bank, crucial for regeneration of species following disturbance. On the other hand, a greater seed reserve may enhance the abilities of larger seeds to persist by providing for metabolic requirements during quiescence period, until suitable light or moisture conditions arise. However, the large seeded primary forest species are relatively immobile because of low dispersal efficiency (Wunderle 1997).

Seed size is genetically determined and there exists a wide intergeneric and interspecific variation. Various climatic factors, such as temperature, humidity, light, soil characteristics, dispersal syndromes, germination time, densities of competing plants, herbivores and fungi, that differ among habitats, affect the production and selection for different seed sizes. Compared to smaller seeds, large and heavy seeds contain larger amounts of reserves to stimulate germination, seedling survival and growth (Milberg & Lamont 1997). Oni and Bada (1992) suggested that seedlings of *Terminalia ivorensis* from larger seeds showed better growth than those from smaller seeds. Milberg and Lamont (1997) suggested that the effect of large seeds was more pronounced in nutrient-impooverished soil. The young seedlings from large-seeded species withdraw nutrients for their successful establishment, survival and early seedling growth more from the cotyledons than from the soil. In nutrient-deficient soils, small-seeded species with smaller cotyledons grew poorly

because early seedling growth is regulated mainly by nutrient uptake from the soil. Small seed size is typically associated with regeneration after disturbance (Fenner 1995). For small-seeded species, successful colonization of newly-disturbed areas depends on rapid germination and a higher rate of seedling growth (Swanborough & Westoby 1996).

Differential concentrations of mineral nutrients in embryos and seed coats could also influence seedling establishment, irrespective of seed size. Among the two species of *Prosopis*, namely *P. cineraria* and *P. juliflora*, seed weights were not significantly different. However, for the native *P. cineraria*, nutrient concentration was higher in the embryo than in the seed coat, while for *P. juliflora* it was higher in seed coat. *P. cineraria* could sustain the growth of slow-growing seedlings for a relatively longer period and could delay the dependence on the external supply to a later stage, while the exotic *P. juliflora* would need immediate nutrient uptake from the soil upon emergence of its fast-growing seedling (Sharma & Dakshini 1996). This favours establishment of *Prosopis juliflora* on newly disturbed or deforested sites. Per cent germination in *Leucaena leucocephala* and *Wrightia tinctoria* decreased when embryos were excised, perhaps due to the removal of the fleshy endosperm which contains the bulk of nutrition used by the germinating seeds as a source of energy (Babeley & Kandya 1986).

Although a positive relation between seedling fitness (i.e. seedling establishment) and seed size has been generally assumed, Ganeshiah and Uma Shaanker (1991) found that seed size represented a trade-off between seedling establishment and seed dispersal efficiency in a wind dispersed tree, *Butea monosperma*; the small seeds may pack more fat than protein or carbohydrate for maintaining the energy level (Lokesha *et al.* 1992).

Scant attention has been paid to the variation in the size and shape of seeds within species and its implications. Seed polymorphism shown by several dry tropical species such as *Lagerstroemia parviflora* (Shukla & Ramakrishnan 1981), *Albizia procera* and *Cassia glauca* (Kandya 1990) increases the potential of the species to colonize due to the existence of different seed types within the same individual with different requirements for germination so that a single species is able to colonize a wide range of environmental situations. A close relationship within species between seed size and/or weight and germination percentage has been documented for many tropical tree seedlings (Table 3). Although improved seed germination and survival are generally attributed to large seed size, medium-sized seeds germinated faster in *Acacia mellifera* (Srimathi *et al.* 1991), and small seeds in *Santalum album* and *Lagerstroemia parviflora* (Prasad *et al.* 1988).

Genetic variability

Several dry tropical species have a wide geographical distribution and have genetically adapted to different environmental conditions found within their historic range.

Table 3 Effect of seed size and/or seed weight on germination of certain dry tropical tree species.

Species	% Germination		Source
	Heavy/large seeds	Light/small seeds	
<i>Cassia glauca</i>	74	64	Kandya (1990)
<i>Cassia siamea</i>	36	25	Kandya (1990)
<i>Ceiba pentandra</i>	15	11	Dileep <i>et al.</i> (1994)
<i>Dillenia indica</i>	32	21	Singh and Khan (1998)
<i>Holoptelia integrifolia</i>	39	18	Prasad and Jalil (1991)
<i>Kydia calyciana</i>	47	13	Negi and Todaria (1997)
<i>Leucaena leucocephala</i>	76	55	Gupta <i>et al.</i> (1983)
<i>Peltrophorum ferrugineum</i>	14	5	Kandya (1990)
<i>Terminalia bellirica</i>	100	23	Negi and Todaria (1997)
<i>Terminalia chebula</i>	47	33	Negi and Todaria (1997)
<i>Terminalia tomentosa</i>	57	13	Negi and Todaria (1997)

Populations of such species show differential provenance-related germination and seedling growth responses.

Variations in percentage germination and rate of seedling growth among provenances have been observed in several Indian dry tropical species such as *Prosopis cineraria* (Arya *et al.* 1995), *Albizia lebeck* (Roy 1985), *Lagerstroemia parviflora* (Prasad *et al.* 1988) and *Acacia nilotica* (Krishnan & Toky 1995a).

Variation in seedling growth among provenances has also been reported from other dry tropical parts of the world. The mean annual increment of height and diameter of seedlings of *Acacia mangium* varied among 19 provenances from south-east Asia, China, Bangladesh, Australia and Fiji (Harwood & Williams 1991). In addition to growth, seedlings from different provenances also show variation in stress resistance. For example, variation in frost and disease resistance was found in seedlings of *Casuarina cunninghamiana* from 13 Australian localities (Merwin *et al.* 1995). Also, seedlings of *Dalbergia sissoo* from Nepal were more resistant to rust fungi compared to those from Pakistan (Neil 1990). In Chile, out of 32 provenances of *Eucalyptus globulus*, seedlings from south-east Tasmania, Cape Barren Island, Flinders Island and Victoria performed better (Infante & Prado 1991). Sun and Dickinson (1997) suggested that tropical provenances of *Eucalyptus camaldulensis* were more suitable than those from the subtropical ones.

Differences in the capacity of N₂ fixation were reported for *Acacia albida* provenances (Sanginga *et al.* 1990). In *Casuarina cunninghamiana* (Fleming *et al.* 1988) and *Casuarina equisetifolia* (Sougoufara *et al.* 1987) significant differences in the N₂-fixing ability have been found among clones of the same species inoculated with *Frankia* strains in glasshouse conditions. Nodulation was highly variable among provenances of *Acacia auriculiformis* (Ngulube 1990). Of the 18 Indian provenances of *Acacia nilotica* tested, the Sirsa provenance showed maximum nodulation and nitrogen fixing ability, and this was mainly attributed to genetic effects and particular provenance – *Rhizobium* combination (Beniwal *et al.* 1995).

Characteristics like pod length and seed weight, which indicates the amount of seed reserve, also varied among provenances in *Tecomella undulata* (Arya *et al.* 1993), *Albizia*

lebeck (Kumar & Toky 1993), *Prunella vulgaris* (Bagchi & Dobriyal 1990) and *Acacia mangium* (Salazar 1989).

Variations in nutrient contents of plants among provenances were observed for *Acacia albida* (Sniezko & Stewart 1989). Carbohydrate, chlorophyll, N, P, K, Ca and Mg contents of leaves of *A. nilotica* varied significantly among provenances. The provenance showing the highest carbohydrate content in leaves also had the maximum chlorophyll concentration in *Acacia nilotica* (Krishnan & Toky 1995b). Seeds of *Albizia lebeck* from Cochin and Madurai, compared to those from other places, had maximum carbohydrate content which increased the seedling survival and growth under stress from frost and drought (Kumar & Toky 1994). Likewise, the provenance showing the highest protein content in leaves had the highest photosynthetic rate and hence productivity in *Populus bolleana*, *Populus alba* (Kazaryan 1985) and *Leucaena leucocephala* (Arora *et al.* 1986).

Soil moisture

Soil moisture availability is a key factor influencing the growth and survival of plant communities in tropical dry forests (Lugo *et al.* 1978). Seeds of a majority of dry tropical species mature in summer and are dispersed at the beginning of the rainy season when sufficient moisture is available for germination and seedling growth (Singh & Singh 1992). However, if seeds fail to germinate during the first rainy season, as in *Diospyros melanoxylon* (Ghosh *et al.* 1976), their germination is delayed until the second wet season. Because the dry tropical species have historically experienced unpredictable droughts, at least a few of them possess the ability to germinate under conditions of substantial water stress, for example *Acacia farnesiana* (–0.10 MPa; Scifres 1974), *Acacia senegal* (–1.38 MPa; Palma *et al.* 1995), *Acacia tortilis* (–1.0 MPa; Coughenour & Detling 1986), *Cassia obtusifolia* (–0.5 MPa; Daiya *et al.* 1980) and *C. occidentalis* (–0.5 MPa; Daiya *et al.* 1980). *Leucaena leucocephala* seeds germinate at water potentials between 0 and –1.6 MPa, however the percentage and rate of germination decreased with further increase in water stress (Cavalcante & Perez 1995).

Ray and Brown (1995) hypothesized that germination and survival of young seedling recruits of Caribbean dry forest species were closely linked to rainfall quantity and timing, and in a region typified by a long dry season, seedling desiccation may indeed be a major obstacle to recruitment. Seedling mortality in yellow mallee (*Eucalyptus incrassata*) was restricted to dry summer months of the year and this mortality could be reduced by an increase in soil moisture (Wellington & Noble 1985). Recruitment of *Acacia tortilis* seedlings was confined to years with relatively high precipitation (Skoglund 1992). Intermittent recruitment in *Acacia victoriae* may be the result of high seedling mortality, rather than infrequent germination (Grice & Westoby 1987). Germination and mortality were highly seasonal in the 53 species examined from the tropical dry forest of Ghana, mortality being highest in dry periods (Lieberman & Li 1992). For certain species, microsites with both high moisture availability and low root competition seem to be more decisive for recruitment (Gerhardt & Hytteborn 1992). Limitation of growth by water due to frequent drought periods may interact with limitation by other factors. For example, N and P might be limited as the rate of N mineralization is dependent upon soil water status (Marrs *et al.* 1991).

Several species do show plasticity and ability to acclimatize to moisture-deficient conditions. An increase in root to shoot dry mass ratio and a greater allocation of dry mass to lateral roots, in species such as *Drypetes parvifolia* and *Teclea verdoornia* (Lieberman & Li 1992), enhanced the root surface area available for water uptake (Wright *et al.* 1992). Ramachandra *et al.* (1997) found that seedlings of *Acacia catechu* from drier regions showed higher leaf chlorophyll content compared to those from humid regions. Also, the decrease in chlorophyll content due to imposed water stress was smaller in seedlings from dry region seed sources than those from humid region sources. Leaves of seedlings from hot and drier regions close their stomata during the day, to check the transpirational loss, and photosynthesis is largely confined to sunrise and sunset hours, in other words cooler periods of the day when light intensity is low. Evidently in such cases, high chlorophyll content compensates for the low light intensity.

In the rainy season, when most of the tree seeds germinate, the seedlings, particularly in open forests, face competition from annual herbaceous flora which germinate at the same time. However, in subsequent dry seasons, the annual species die off and act as a mulch, which helps to conserve the soil moisture and to protect the seedlings from harsh sunlight. Mulching increased seedling establishment in *Dalbergia sissoo*, *Acacia catechu* and several other dry tropical species in the Singrauli mine spoil area of India (Singh *et al.* 1996).

Temperature and fire

Occurring in areas characterized by a markedly warm to hot

season within the annual cycle, and frequent fires which occur naturally or anthropogenically (Goldammer 1993), the dry forest species are fairly tolerant to moderately high temperatures at all life cycle stages. However, even species localized in restricted geographical areas may differ in the optimal temperature requirement for germination. For a majority of the dry deciduous Afrotropical forest species, the optimum temperature for seed germination was between 20 and 25°C, while for a few, germination was highest at 30°C (Teketay & Granstrom 1997). The optimum temperature for seed germination was 30°C for *Acacia karoo*, 25°C for *Acacia tortilis* (Choinski & Tuohy 1991), 30°C for *Cambretum apiculatum* (Choinski & Tuohy 1991), 30°C for *Entoda abyssinica* (Teketay 1996), 25°C for *Hancornia speciosa* (Oliveira & Valio 1992) and 20°C for *Populus ciliata* (Sah & Singh 1995). For certain Ethiopian dry forest species, for example *Abutilon longioupse*, *Croton macrostachyus* (Teketay & Granstrom 1997) and *Erythrina burana* (Teketay 1994), seed germination was inhibited at low temperature (10°C), while for several other species such as *Lobelia giberroa*, germination was inhibited at 30°C. Germination of hard seeded scarified seeds of a few species such as *Acacia abyssinica* progressively increased with temperature up to 30°C. Marked diurnal fluctuation in temperature that occurs in gaps or open canopied sites, may enhance germination in certain woody climbers such as *Ureia hypselodendron* and tree species such as *Veronica amygdalina* (Teketay & Granstrom 1997). Gill (1985) suggested that the large fluctuation in temperature experienced by seeds of *Acacia cyclops* deposited in open sunny sites contributes to the breaking of physical dormancy. Teketay (1998) argued that a wide range of alternating temperature may indeed signal the formation of gap or overhead open-canopied area to the seeds. Immediate appearance of *Acacia melanoxylon* seedlings due to removal of mature plants indicated the response of seeds to an increase in amplitude of diurnal fluctuation in temperature (Farrell & Ashton 1978).

Seeds are released from dormancy by heat shock generated by fire in several Ethiopian leguminous tree species occurring between 0 and 2400 m elevation (Teketay 1994, 1996) and in *Acacia sieberiana* and *A. gerrardii* of the dry savanna in Uganda (Mucunguzi & Oryem-Origa 1996). Heat shock-stimulated germination is widespread in families like Fabaceae, Rhamnaceae, Convolvulaceae and Sterculiaceae (Bell *et al.* 1993). There are species which show higher percentage germination when exposed even to fire-generated smoke. Brown and van Staden (1997) reported that smoke priming can be used as a technique to maximize seed germination for *ex situ* conservation of many rare and threatened African fynbos species experiencing repeated fires. Aerosol smoke and smoke water treatments resulted in significant germination response from the soil seed bank in unmined forest soils and rehabilitated bauxite mine soils in Western Australia (Roche *et al.* 1997).

On the other hand, seeds of *Acacia aneura*, *Cassia nemophila* and *Dodonaea viscosa* at 0, 1, or 2 cm depth in the soil were killed by slow burning litter fire when temperature

exceeded 80°C (Hodgkinson & Oxley 1990). Intense heat due to fire, even for brief periods, might be lethal and kill seeds, for example after 1.5 min at 290°C in *Eucalyptus obliqua*, 4 min at 380°C in *Leptospermum juniperinum* (Ashton 1986), 15 s at 350°C in *Eucalyptus regnans*, 15 s at 600°C in *Leptospermum laevigatum*, and 15 s at 500°C in *L. myrsinoides* (Judd 1993).

Since almost all the dry tropical forests are burnt annually, several tree species have developed strategies to avoid the possible deleterious effect of fire on their regeneration. For example, fruits of the dominant dipterocarp tree species of dry forest in Thailand, such as those in the genera *Shorea* and *Dipterocarpus*, are dispersed by wind after the peak season of fires, and germinate at the beginning of the wet season (Stott 1988). The analysis of historic information from India revealed that during the last century and early this century almost all Indian deciduous forests were burned every year (Goldammer 1992). Indian teak (*Tectona grandis*) forest is known to exhibit stimulated regeneration in burnt compared to fire-protected areas, as fire stimulates seed germination and facilitates establishment. Only weak seedlings are killed outright by fire, and sufficient seedling stock accumulates even with annual fires to establish populations of fire-hardy seedlings (Champion & Seth 1968). Seedling growth and resistance to fire are also correlated with available soil moisture. Seedlings of *Pterocarpus angolensis* which escaped fire developed an extensive root system to compete for water (Strang 1966). Nevertheless, repeated burning late in the dry season killed most of the seedlings and saplings in dry African woodland (Menaut *et al.* 1995). As a result of fire, seeds start to take up water and germinate, but when this germination time synchronizes with the conditions which are deadly to seedlings, seeds sprout and die, thus depleting the natural seed bank.

Light

Germination, survival and seedling growth responses to light intensity vary markedly among species. *Toona ciliata* and *Adina cordifolia* showed higher germination percentage in shade or under mulch than in the open (Beniwal *et al.* 1990a, b). The rate of germination varied under different light regimes in most of the examined species of the dry forest of Ethiopia (Teketay & Granstrom 1997). For example, darkness and leaf shade (R:FR [red light: far-red light] = 0.08) inhibited germination, respectively in *Lobelia giberroa* and *Veronica amygdalina*. In contrast, seeds of *Pittosporum viridiflorum* showed a significantly lower germination in daylight (R:FR = 1.12) compared to neutral shade and leaf shade (R:FR = 0.08). On the other hand, for most of the species of Caribbean dry forest, germination success was approximately equal in shaded and unshaded sites. Shade did, however, markedly influence the survival of seedlings of these species. Ray and Brown (1995) were able to categorize these Caribbean dry forest species into three groups, namely (1) those unlikely to survive without medium shade (25% of

full sunlight), for example *Guettarda parviflora* and *Coccoloba microstachya*, (2) those showing weak survival without medium shade and greatly increased survival in medium shade, for example *Guaiacum officinale* and *Sabinea florida*, and (3) those showing good survival without medium shade but enhanced survival in medium shade, for example *Plumeria alba* and *Bursera simaruba*. Ray and Brown (1995) argued that shade demand for survival integrates drought tolerance and light requirement, allowing seedlings to avoid very high light intensity and very low moisture. Although seedlings of all tropical deciduous species of Mexico examined achieved higher growth rates and net assimilation rates in the high light treatment (400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, i.e. light available in a medium-sized gap) than at low light intensity (80 $\mu\text{mol m}^{-2} \text{s}^{-1}$, i.e. the light underneath the vegetation canopy during the rainy season), the pioneer or gap-requiring species *Heliocarpus pallidus* and *Apoplanesia paniculata*, which possessed smaller seeds sustained a faster growth rate under high light intensity than persistent or shade-tolerant species such as *Amphipterygium adstringens*, *Caesalpinia eriostachys* and *Caesalpinia platiloba*, which possessed larger seeds (Rincon & Huante 1993). Seedling growth in *Dalbergia sissoo* and *Acacia catechu* was maximum in low shade treatment, while *Casuarina equisetifolia* exhibited maximum growth in an unshaded treatment (Saxena *et al.* 1995).

Soil nutrients

Most dry tropical forest soils are nutrient poor (Sanchez 1976; Singh *et al.* 1989). Increase in the growth of tree seedlings due to nitrogen application has been reported for most species examined in India, including, *Populus ciliata* (Deol & Khosla 1983), *Eucalyptus tereticornis*, *Eucalyptus camaldulensis*, *Eucalyptus grandis* and *Eucalyptus citriodora* (Prasad & Rawat 1994), *Acacia mollissima* (Rao 1985), *Acacia catechu* (Prasad & Rawat 1992), *Bauhinia variegata* (Koul *et al.* 1995) and *Leucaena leucocephala* (Sivasupiramanium *et al.* 1988). Rachmawali *et al.* (1996) reported urea-induced increases in most of the growth variables for seedlings of several Indonesian species, such as *Casuarina junghuhniana*, *Albizia lebeck*, *A. procera*, *Dalbergia latifolia* and *A. sinensis*. However, there appears to be a limit to the quantity of N applied which can increase the seedling growth. For example, graded doses of N increased biomass of *Eucalyptus tereticornis* seedlings from control to 100 ppm N per pot and thereafter the biomass decreased with further increase in the N level (Prasad & Rawat 1994). An antagonistic effect of N at higher doses may also cause lower uptake of P and K by the seedlings (Koul *et al.* 1995). Exogenous application of P increased collar diameter and root length, and other growth characteristics in *Sesbania sesban* (Dutt & Pathania 1986), *Bauhinia variegata* (Koul *et al.* 1995), *Dalbergia nigra* (Chaves *et al.* 1995) and *Leucaena leucocephala* (Prasad & Rawat 1992). P application increased P content in *Terminalia ivorensis* (Aluko & Advayi 1983), but decreased N and K contents in

Table 4 Increase in biomass and leaf area of certain dry tropical seedlings under elevated CO₂.

Species	Duration of exposure (days)	Biomass (%)	Leaf area (%)	Source
<i>Acacia auriculiformis</i>	90	44	85	Devakumar <i>et al.</i> (1996)
<i>Annona squamosa</i>	90	35.5	320	Devakumar <i>et al.</i> (1996)
<i>Artocarpus integrifolia</i>	90	155	340	Devakumar <i>et al.</i> (1996)
<i>Dalbergia latifolia</i>	90	36	71	Devakumar <i>et al.</i> (1996)
<i>D. sissoo</i>	90	193	270	Devakumar <i>et al.</i> (1996)
<i>Derris indica</i>	90	135	235	Devakumar <i>et al.</i> (1996)
<i>Eucalyptus camaldulensis</i>	84	75	21	Wong <i>et al.</i> (1992)
<i>E. citriodora</i>	90	51	35	Devakumar <i>et al.</i> (1996)
<i>E. cypellocarpa</i>	84	85	27	Wong <i>et al.</i> (1992)
<i>E. grandis</i>	42	275	-	Conroy <i>et al.</i> (1992)
<i>E. pauciflora</i>	100	212	117	Wong <i>et al.</i> (1992)
<i>E. pulverulenta</i>	84	158	71	Wong <i>et al.</i> (1992)
<i>Fagus grandifolia</i>	60	83	92	Bazzaz <i>et al.</i> (1990)
<i>F. sylvatica</i>	105	54	40	Overdieck (1993)
<i>Feronia elephantum</i>	90	17	45	Devakumar <i>et al.</i> (1996)
<i>Ficus obtusifolia</i>	90–100	10	35	Ziska <i>et al.</i> (1991)
<i>Hevea brasiliensis RR11</i>	105	17	32	Devakumar <i>et al.</i> (1998)
<i>Liriodendron tulipifera</i>	168	22	-15	Norby and O'Neill (1991)
<i>Piper auritum</i>	111	15	5	Reekie and Bazzaz (1989)
<i>Spathodia campanulata</i>	90	88	216	Devakumar <i>et al.</i> (1996)
<i>Swietenia microphylla</i>	90	101	53	Devakumar <i>et al.</i> (1996)
<i>Tabebuia rosea</i>	-	164	83	Ziska <i>et al.</i> (1991)
<i>Tamarindus indica</i>	90	12.3	27	Devakumar <i>et al.</i> (1996)
<i>Tectona grandis</i>	90	460	1012	Devakumar <i>et al.</i> (1996)
<i>Zizyphus jujuba</i>	90	125	256	Devakumar <i>et al.</i> (1996)

Eucalyptus grandis (Prasad *et al.* 1984), *Acacia mollisima* and *Celtis australis* (Rao 1985).

Combined application of N and P significantly increased total dry weight and stem and root weights of seedlings of *Leucaena leucocephala* (Dutt & Pathania 1986), *Adenanthara pavonia*, *Albizia falcataria* and *Schleimitzia insularum* (Moloney *et al.* 1986), *Bauhinia variegata* (Koul *et al.* 1995), and *Acacia catechu* and *Prosopis juliflora* (Prasad & Rawat 1992). NPK application increased specific leaf area (SLA), leaf area ratio (LAR) and relative growth rate (RGR), but decreased biomass allocation to roots in seedlings of 34 woody species from a dry deciduous forest of Mexico (Huante *et al.* 1995).

Enhancement of seedling growth due to nutrient amendment (120 kg N, 60 kg P and 60 kg K ha⁻¹) was observed in several species when grown in pot culture with mine spoil as a medium (Singh *et al.* 1996). Shoot growth was particularly accelerated in *Acacia nilotica*, *Albizia lebeck*, *Azadirachta indica*, *Butea monosperma*, *Dalbergia sissoo*, *Dendrocalamus strictus*, *Ficus* spp., *Gmelina arborea*, *Grewia hirsuta*, *Madhuca indica*, *Morus alba*, *Pongamia pinnata*, *Terminalia arjuna*, *Terminalia bellirica* and *Zizyphus jujuba*. Impact of fertilization was less on leguminous species (for example *Acacia catechu* and *Albizia lebeck*) compared to non-legumes (for example *Tectona grandis*, *Terminalia bellirica*, *Gmelina arborea* and *Azadirachta indica*) transplanted on mine spoil. Interplanting of leguminous tree seedlings (for example *Dalbergia sissoo*) increased shoot growth of non-leguminous species (for example *Holoptelia integrifolia*), indicating the

impact of nitrogen input through symbiotic N-fixation (Singh *et al.* 1996).

Availability of nutrients, particularly of P, to seedlings, is enhanced by mycorrhizal association which could also improve water relations. Vijaya and Srivasuki (1997) reported that inoculation with *Glomus fasciculatum* increased per cent root colonization and seedling growth in *Albizia amara*, *Tamarindus indica*, *Dalbergia sissoo*, *Derris indica* and *Pterocarpus santalinus*. The enhancement of dry matter yield in all of the above species was more than two-fold over control. Seedlings of *Tectona grandis* showed about 126% increase in dry weight over control when inoculated with *Glomus mosseae* (Durga & Gupta 1995). Gupta *et al.* (1997) worked on 27 vesicular arbuscular mycorrhizae (VAM) inoculants for screening suitable fungi inoculant for *Cassia fistula*. They found that inoculation with *Glomus versiforme*, increased dry biomass of shoot, number of leaves and leaflets per plant by 265, 36 and 55%, respectively over control. Certain other dry tropical species of India showing significant increase in seedling growth when inoculated with mycorrhizal fungi are *Terminalia bellirica*, *Azadirachta indica* (Mohan *et al.* 1995) and *Casuarina equisetifolia* (Sambandan *et al.* 1994). Increase in seedling growth due to inoculation of VAM fungi was also reported in *Dalbergia nigra* (Chaves *et al.* 1995) and *Leucaena leucocephala* (Ojeda *et al.* 1995). However, most species in African dry forest did not require inoculation when planted, because VAM fungi were already present in grass root systems and could therefore be shared by the tree seedlings (Hogberg 1992).

Ambient CO₂

The projected doubling of atmospheric concentration of CO₂ and associated processes could strongly affect seedling growth (Eamus & Jarvis 1989; Ceulmans & Mousseau 1994). Various physiological processes such as photosynthesis, water use efficiency and whole plant growth are known to be modified by elevated CO₂ (Johnsen & Major 1998; Drake *et al.* 1997). Increase in percentage biomass and per cent leaf area under elevated CO₂ in seedlings of several dry tropical trees have been reported, but the response to elevated CO₂ differs among species. Short-term exposures to enhanced CO₂ have resulted in 5–1000% increase in leaf area, and 10–460% increase in biomass of seedlings (Table 4).

Predators and parasites

The effect of predators and pathogens on seeds and seedlings could be both deleterious and advantageous, depending upon the kind, intensity, site of predation and also the type of seed. Janzen (1981) found that of the 975 species in Guanacaste province, at least 100 regularly had beetle larvae that develop and kill the seeds. Joshi *et al.* (1990) have listed the insect pests of dry forest seeds of north east and central India. Seed deterioration in *Albizia lebbek* is mainly due to the insect borers *Bruches bilineatopygus* and *B. sparsemaculatus* and a fungus *Fusarium pallidorozeum* (Harsh & Joshi 1993). Seeds may have evolved thick seed coats as defensive structures for preventing penetration of insect ovipositors, and phenolic compounds in the seed coat contribute to inhibition of microorganism growth (Mohamed-Yasseen *et al.* 1994).

Dry forests are usually characterized by a higher proportion of wind dispersed species compared with moist forest (Bullock 1995; Gentry 1995). For example, in neotropical dry forest, wind-dispersed genera such as *Serjania* and *Lonchocarpus* are more preponderant and account for one-third to one-quarter of tree species (Gentry 1995). In the dry forest of Charallave, Venezuela, about 30.5% of phanerophytes, such as *Ceiba pentandra*, *Tabebuia ochracea* and *Terminalia* spp., are anemochorous (Wikander 1984). In a Guanacaste dry forest, however, 65% of the tree species were dispersed by animals and only 25% by wind (Janzen 1988b). Most of the dry forest mammals and birds rarely visit pastures with little or no remnant woody vegetation (Guevara 1986). In a 12-year old abandoned pasture in Guanacaste National Park, with a species-rich mature forest at 200 m distance, natural regeneration was still dominated by wind-dispersed tree species (Janzen 1988b). Thus, secondary succession on such abandoned pastures may be enhanced by the introduction of seedlings of animal-dispersed tree species (Gerhardt 1993). Compared to wind or water-dispersed species, fruits of animal-dispersed species showed 4–6 fold higher accumulation of proteinase inhibitors at their peak growth stage to prevent dispersers from removing premature fruits, and low or negligible accumulation at the ripened stage to encourage fruit removal by dispersers (Hebber *et al.* 1993).

In Mesoamerican dry tropical forests, vertebrates can act as predispersal/post dispersal predators (Dirzo & Dominguez 1995). For example, at Chemela, when seeds of *Erythroxylum havanense* were placed on the ground with and without protective enclosures for vertebrates; the protected seeds had a 3.7 times higher chance of successful establishment (Gryj 1990). It is possible that selection may favour plants with animal-dispersible fruits when frugivores are common, and those with competitive seedlings when fruit-eating mammals are rare (Howe & Smallwood 1982).

Inferences for forest management

Dry tropical forest occurs in regions experiencing extended dry periods within the annual cycle and frequent severe droughts, which may have conditioned the physiology, phenology, reproductive and successional patterns of the component species populations. This forest once covered more than half of the world's tropics, but has now significantly receded due to human activities. Knowledge of the ecological requirements at seed and seedling stages may be useful for structuring the conservation and restoration processes so as to maximize the persistence and retention of required species. The information available on these aspects is rather disjointed and permits only a few pragmatic as well as intuitively satisfying generalizations.

Due to the presence of diverse species complements in different segments of the dry tropical environmental gradient, and spatial and temporal variations in microsites within a site, there is a marked diversity in size, viability, dormancy patterns, and seasonality in the production and germination of seeds. Most of the studies on germination and seedling growth, however, have been laboratory-oriented and may have limited correspondence with real life. Coordinated, long-term field-based studies are needed for identification of multiple cues and niches for germination. Knowledge of the volume of seed crop and its contribution to persistent seed bank, and the factors which stimulate the seed banks to produce successive populations of seedlings, is required for the perception of future composition of the forest and for developing techniques for manipulation of microhabitats for the establishment of the desired suite of species on a site.

Gap-requiring early-successional fast-growing species with small seeds have higher light demand and greater drought tolerance than large seeded late successional, which demand shade for survival of seedlings. The shade demand also integrates the need to avoid high temperature and high moisture stress. Thus restoration efforts should include seeding or introduction of seedlings of desired species under existing canopies. Alternatively, successful species introductions could be done along a time gradient by first developing a cover crop of fast-growing pioneer, preferably of leguminous species. Seedlings that develop some physiological and morphological adaptive characteristics to water stress, for example increased root to shoot dry mass, can account for greater success in restoration efforts. The recovery process

can be accelerated by selecting large seeds of desired species for seeding because they contain high concentrations of mobilizable reserves which influence early performance of seedlings in nutrient-poor and water-stressed soils. Pot culture and a few field experiments have indicated a positive impact of chemical fertilization on seedling growth. However, developing a leguminous cover crop or interplanting with leguminous species and inoculating the seedlings with appropriate mycorrhizal strains may constitute a more successful low-input strategy for removing the limitations due to N and P shortages.

Although most of the dry forests of the world are burnt frequently, there is a conspicuous lack of studies on seed and seedling dynamics in response to pre- and post-fire events. In a highly damaged area, the historic pattern of disturbance and successional processes can be used as a template for restoration plans. For specially fire-prone areas, hard-seeded taxa that develop extensive root systems for water extraction, or those that can avoid fire effects due to asynchrony of seed dispersal and fire events, and those that retain regeneration capacity in their burned shoots, may have a greater probability of success. Extensive field-based knowledge at species and community levels is needed to permit biodiversity manipulations of biotic components such as introduction of seed dispersers to increase the area of seed deposition of desired plant species, and of seed predators for suppressing the alien/invaser species.

Healthy seeds and seedlings are a prerequisite to any restoration effort. More studies on seed longevity, nature of seed dormancy, optimal temperatures for germination and conditions for storage of seeds so as to reduce the loss of viability, and pretreatments for releasing the seeds from dormancy without affecting post-germination seedling vigour, are needed, as a considerable between-species diversity in these characteristics has been shown to exist. A positive influence of short-term exposures to elevated CO₂ and of exogenous inputs of N and P can be used for producing bigger seedlings for introduction into forests. Within-species genetic variation leads to production of seeds which give rise to seedlings of variable mineral content, nitrogen-fixing ability, and growth pattern. Selection of provenances performing best on a site should be a prerequisite for any restoration effort.

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