Ecology of tree seed and seedlings: Implications for tropical forest conservation and restoration

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Seed and seedling traits vary strongly across the tropical forest biome to cope with the variations in the distribution and amount of rainfall, light, temperature and soil nutrient regimes, and the intensity of predation and disturbance. Proportion of species producing dormant seeds increases along a gradient of dryness and unpredictability of rainfall. Seed longevity is generally higher for dry tropical than for wet tropical species. Environmental variables and the dispersal syndrome have led to the selection for and production of different seed sizes, with implications for germination and seedling establishment in different situations, and for the build up of persistent soil seed bank. Seeds have evolved mechanisms to recognize environmental cues which enable them to confine their germination in particular periods and locations to allow for a greater probability of seedling establishment and survival. While for a majority of wet tropical species gap dependency and shade tolerance are important, seedlings of many dry tropical species show shade dependence. Successional hierarchy is frequently reflected in ecological requirements for germination and seedling fitness. Field microsites represent multiple-variable cues for germination and establishment. Knowledge on the ecology of germination and seedling growth is vital, not only for understanding the community processes of plant recruitment and succession, but also for developing strategies for the conservation of biodiversity and restoration of tropical forests.

TROPICAL forest, a storehouse of biodiversity, accounts for 52% of the total forest area of the world, of which 42% is dry forest, 33% is moist forest and 25% is wet and rainforest[1]. With a decrease in rainfall, the wet evergreen rainforest changes into moist deciduous, which with further decrease in rainfall gives way to dry deciduous forest[2]. Dry forest is next to rainforest in ecological complexity which arises mainly due to strong seasonal and inter-annual variability in rainfall, permitting the occurrence of equally variable suites of species. In the rainforest, the constantly high temperatures and predominantly moist environment have selected seed traits for achieving mainly the reproductive and dispersal function[3]. The cyclical perturbation due to the pronounced seasonality in the tropical dry forest allows seasonal germination and establishment with different consequences for size–age population distribution and community structure[4]. Native species of the forests are able to sense several environmental conditions simultaneously and confine their germination and emergence to particular periods of the year and habitat locations for successful establishment and survival[5]. Knowledge on germination and seedling establishment is of pivotal importance for understanding such community processes as plant recruitment and succession and for the management of plant populations.

In recent years, increasing proportions of tropical forest have been modified into more open secondary forest or savanna, or have been completely destroyed through such activities as agriculture or mining. This extensive deforestation and habitat conversion is recognized as the biggest factor in the present biological diversity crisis[6]. Models of habitat loss suggest that this process may produce an extinction debt, a pool of species likely to go extinct, unless the habitat is repaired or restored[7]. Manipulation of the initial composition of species must be undertaken for obtaining the desired direction of successional processes[8]. Inclusion of native remnant trees within restoration areas may enhance local deposition of wind-dispersed tree seeds and serve as movement corridors for seed-dispersing birds[9–11]. Also, the presence of trees may facilitate the growth and survival of forest plants by ameliorating local microclimatic conditions[9,12], improving soil chemical and physical properties[12–14] and suppressing aggressive grasses that could compete with forest seedlings[13,15]. The knowledge on seed germination and seedling growth is therefore, necessary for the success of efforts on augmentation, introduction and re-introduction of tree populations.

Although information on the ecological requirements at the seed and seedling stages is vital both for conservation and rehabilitation, the same is seldom articulated in silvicultural and forest management plans[16]. We review here those aspects of germination and seedling growth of tropical forest trees, which we feel are extremely relevant to biological conservation and restoration. The review follows the scheme outlined in

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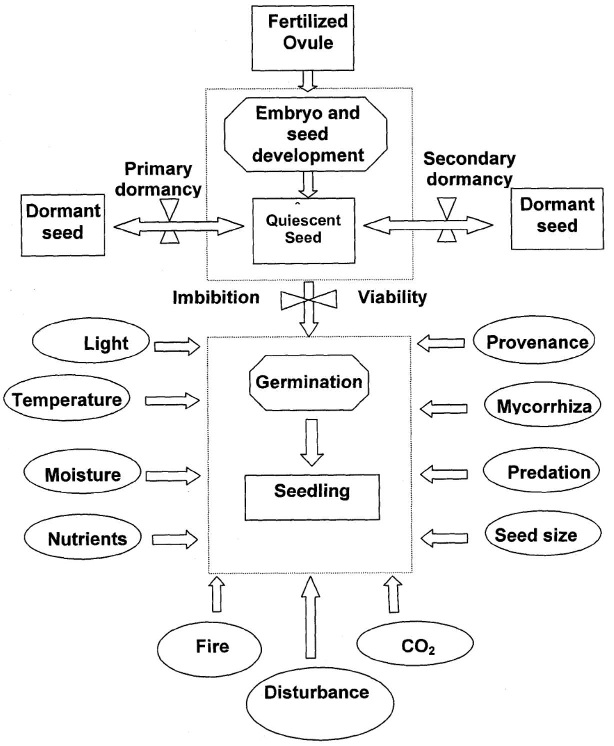

Figure 1. Fertilized ovule-to-seedling continuum. The top dotted-box represents the process of histodifferentiation of fertilized ovule into quiescent seed. The seed may show primary dormancy due to hard seed coat, immature embryo or presence of inhibitors or develop secondary dormancy when exposed to conditions not favourable for germination. The bottom dotted-box represents the process of seeding formation and growth from quiescent seed, and the abiotic and biotic variables which influence the process.

Figure 1 which shows the major processes and the major intrinsic and extrinsic variables to which the seeds and seedlings are exposed. Some of the earlier reviews on topics of interest are those of Foster[17], Grubb[18] and Janzen[19].

Seed viability, germination and dormancy

In essence, seed is a miniature tree because it is responsible for its regeneration and ultimately for its reproductive success. Following fertilization, growth sets in various parts of the ovule resulting into a seed; the zygote develops into the embryo, the primary endosperm nucleus gives rise to endosperm and the integuments form the protective seed coat, which is the seed's primary defence against adverse environmental conditions[20]. The quiescent seeds readily germinate under favourable conditions, while others may possess primary dormancy or develop secondary dormancy that may require treatments to shift the seed again from the dormant to the quiescent state[21].

Seed viability is the ability of the seed to remain germinable. Seeds are classified into two categories on the basis of their viability – orthodox and recalcitrant[22]. Orthodox seeds are usually dormant and can retain their viability for longer periods even under fully hydrated oxygenic condition, while recalcitrant seeds exhibit little or no dormancy and cannot be dried below a critical moisture content. Compared to dry forest, rainforest seeds generally exhibit reduced longevity (i.e. short viability) and rapid germination[23,24]. Most of the Malaysian dipterocarp species exhibit reduction in germination rate as early as one week after release[25]. Fleshy seeded legumes of Central American and south-east Asian rainforests also must germinate within several weeks or die[26].

Seed dormancy is a condition of delayed germination and can be categorized into induced, innate and enforced types[27]. Seed dormancy is particularly associated with environments characterized by variable rainfall trends and with extended dry periods within the annual cycle. Within the tropical forest biome, the proportion of species producing non-dormant seeds declines with a decrease in the predictability and total amount of rainfall and an increase in the length of the dry season. Thus while as many as 63% of the tropical rainforest species produce non-dormant seeds, only 24% of the dry tropical tree species produce seeds which are not dormant (calculated from ref. 28).

Physical dormancy is more prevalent in dry tropical compared to wet tropical species (51% vs 5%, calculated from ref. 28). Seeds may have evolved thick seed coat as defensive structures for preventing penetration of insect ovipositors, and the phenolic compounds in the seed coat contribute to the inhibition of microorganisms[19,20]. Seed-coat dormancy prevents germination during inconsistent isolated showers which may occur in the middle of a long dry season[29]. Individual seeds may become permeable to water at different times, resulting into staggered seedling recruitment which provides 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[30]. Acid, hot water or mechanical scarification are common treatments employed to overcome the seed coat dormancy. Certain animals and microorganisms are also known to break seed dormancy[30]. Seeds of *Acacia senegal* and *Ceratonia siliqua* germinated readily when passed through digestive tracts of goat[31]. In *Gmelina arborea* and *Acacia nilotica*, partial rumination of seeds by sheep and goats enhanced germination[32]. This is due to the action of strong digestive chemicals present in the gut. Termites are also known to break dormancy of *Tectona grandis* fruits[33]. Certain rainforest species such as *Cecropia obtusifolia* showed enhanced germination when passed through bat intestines[34].

Abiotic variables

Light

Seedling emergence and growth in response to changes in quality and intensity of light have received considerable attention. Light stimulates germination in several forest tree species[35] and inhibits in a few[36]. Seeds that require light for germination are called photodormant or positive photoblastic seeds. Positive photoblastism is associated with the preservation of dormancy of buried seeds and/or that of unburied seeds lying beneath green canopies and litter layer. Photoblasticity is due to the presence of phytochrome which is differentially sensitive to red (R) and far red (FR) light[37]. Sunlight passing through a leaf canopy has a low R : FR ratio. Some species require extremely low photon flux density and thus very low R : FR ratio for germination. For example, seeds of *C. obtusifolia*, a rain forest species, buried in soil at a depth of 4 mm, could be stimulated to germinate by exposure to light of only $0.026\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ (ref. 38). Other species require a low R : FR ratio and germinate beneath forest canopies, but not in darkness imposed by burial[37] and in still others, a complete inhibition of germination takes place beneath canopies because of conversion of phytochrome to inactive form[39]. Differences in germinability and seed longevity occurred among neotropical wet forest species under differential light regime[16]. Under closed canopy, seeds of *Simarouba amara*, *Cordia alliodora* and *Vochysia ferruginea* exhibited least longevity and moderate to high germinability, whereas seeds of *Laetia procera* and *Rollinia microsepala* showed moderate longevity, but zero to minimal germinability, and the seeds of *Styphnodendron microstachyum* showed highest longevity but moderate germinability. Thus species that can germinate at high levels in shade can be managed at the seedling stage by opening up the canopy a few months after germination, while those which show little or no germination under closed canopy need canopy removal simply to germinate in adequate numbers[16]. Inhibition of germination under vegetation cover is a mechanism used by species with persistent soil seed banks to detect the formation of a gap[39].

Seedlings of species restricted to and growing rapidly in open and high light areas are called shade-intolerant, while those restricted to close understories are called shade-tolerant[40]. Shade-intolerant species show high specific leaf area (SLA), high leaf area ratio (LAR) and low specific root length (SRL) than shade-tolerant species[41]. Shade intolerance is associated with early rather than late successional species, short rather than long life-span and fast rather than slow growth under low light condition. High SLA and LAR enhance relative growth rate because they confer the ability of high light interception and carbon gain per unit mass invested in leaves[42]. While working on three shade-tolerant tropical moist forest tree species of Panama, viz. *Gustavia superba*, *Virola surinamensis* and *Aspidospermum cruenta*, Molofsky and Fisher[43] reported that gap-grown seedlings grew taller and produced more leaf area than did their understory counterparts. In contrast, according to Kobe[44], the mortality of certain rain forest tree seedlings such as *Trophis racemosa*, *Castilla elastica*, *Pourouma aspera* and *C. obtusifolia* decreased with increase in light intensity (to 20% full sun). On increasing light intensity from 2 to 20% of full sunlight, *Miconia offinis* and *Miconia multispicata* belonging to neotropical rain forest, exhibited higher biomass and leaf area[45].

All examined neotropical species benefited from seed dispersal to light gaps[46]. Some species were restricted as seedlings to gaps, while others persisted, but did not grow appreciably in the shaded understorey. Species like *Aspidosperma cruenta* and *Bombacopsis sessilis* survived equally well in shade and sun with limited growth in shade, while species such as *Ochroma pyramidale* were shade-intolerant. Increase in survival and growth in light is reported for various dipterocarp seedlings[47]. *Shorea robusta*, a nearly-evergreen species showed more active seedling recruitment in old-growth, uneven-aged forest with canopy gaps than in even-aged, young stand having an almost closed canopy[48]. Some tropical dry deciduous species of Mexico associated with disturbed habitats or gaps such as *Heliocarpus pallidus*, *Apoplanesia paniculata*, etc. showed greater light dependency and had rapid relative growth rate under high light intensity. Species associated with undisturbed habitats (dense shade), such as *Amphipterygium adstringens* and *Caesalpinia eriostachys*, showed a smaller increase in relative growth rate with an increase in light[4]. Seedlings of rainforest and those of dry tropical forest, therefore appear to exhibit generally a similar physiological response to light[4]. However, while gap dependency for regeneration is common in tropical wet forest, shade demand or shade dependence of seedlings may be more important than shade tolerance for several species in the dry tropical environment[49]. Seedlings of certain Caribbean dry forest elements survived only in shaded plots, whereas those of others showed a greater survival in shade compared to open condition. Here, shade demand integrates both drought tolerance and light requirement, allowing seedlings to avoid very high light intensity and very low moisture.

Temperature

Optimal temperature for germination may vary from species to species. For example, the native tree species of Western Australia germinate best in a temperature range of 15–23°C (ref. 36), *Populus ciliata* seeds germinate maximally at 20°C (ref. 50) and *Acacia albida* at 25–30°C (ref. 51). Due to great disparity in heat capacity and heat conduction between soil and air, maximum fluctuation in temperature occurs at the surface in gaps away from the insulating effect of vegetation cover. Several tropical species require alternating or high temperatures to break dormancy and a high amplitude of alternating temperatures may indeed signal the formation of a gap to the seeds[52]. A pioneer rain forest species from Mexico, *Heliocarpus donnell-smithii* requires more than 10°C of daily temperature alternation for full germination[53]. An increase in temperature triggers germination by changing the internal enzymatic kinetics and thus the biochemistry of seed cells or by melting the suberized layer in seed coat sclerenchyma or at micropyle, allowing the seed to take up water[53]. Seeds of certain species require a brief period of chilling and subsequent higher temperature for accelerated germination and seedling growth[54].

Soil moisture

Adequate amount of water has to be available for imbibition and subsequent germination, as well as for seedling establishment. In areas with a long dry season, seedling desiccation may be a major obstacle to recruitment[49]. An irrigation experiment in a seasonally dry forest in Panama showed that the availability of soil water during the dry season may limit the survival and growth of seedlings of *Virola surinamensis*[55].

Tree seedlings show several acclimatory responses to water stress. Shortage of water is known to inhibit dry mass allocation to leaves and hence leaf area and leaf growth in seedlings of several rainforest as well as dry forest trees. The reduced leaf growth prevents water loss. Increasing water stress may lead to an increase in leaf thickness which in turn increases the ratio of mesophyll area available for CO_2 uptake per unit leaf area, and hence the water use efficiency for a given transpiration rate. Increase in root to shoot dry mass ratio, decrease in stem weight ratio and increase in net assimilation rate in response to water stress has been observed for seedlings of *Albizia procera*[56]. Mulching is an important part of rehabilitative action for reducing moisture loss in denuded and completely disrupted ecosystems such as mine spoils[57].

Soil nutrients

Growth of tropical tree seedlings is frequently limited by the availability of soil nutrients. N and P are of paramount importance. Increase in the growth of seedlings due to N application has been reported for several tree species, however, exogenous N application beyond a certain dose may be inhibitive[30].

The response of tropical rainforest tree seedlings to P application could vary among pioneer and climax species. For example, increase in dry weight as well as relative growth rate was higher in the pioneer *Tapirira obtusa* compared to the climax species, *Lecythis corrugata*[58]. Significant enhancement in stem volume and overall biomass for *Eucalyptus camaldulensis* planted on oxisol occurred when phosphorus was applied in the form of rock phosphate (in furrows) and single super phosphate (in planting hole)[59]. About 60–70% of the world's tropical rainforest occurs on low fertility oxisols where seedlings may intensely compete with adult trees for light as well as nutrients. Reducing below-ground competition by trenching increased the height of *Aspidosperma carapanauba* (shade tolerater) and *Dinizia excelsa* (light demander) by 330% and 520% and leaf production by 170% and 260%, respectively[60]. Trenching also increased foliar N and P amounts in these central Amazonian species.

Fire

Periodic fire is known to influence the survival of seed, the timing of germination event and the survival of established seedlings[36]. Seeds which are released from dormancy by heat shock or chemicals leached from charred wood as a result of wild fire are called refractory seeds or fire recruiters, and species that are resilient to frequent fire but require fire-free periods for recruitment, possess non-refractory or fire-resister seed syndrome. Species in which seedling recruitment does not occur after fire, but establishment and potential population expansion occur only under fire-free condition are called fire persister or obligate resprouter[61]. A rainforest gap tree, *Ochroma lagopus*, showed enhanced germination when exposed to superficial fire[62]. *Tectona grandis* is known to exhibit stimulated regeneration in burnt than in fire protected areas, as fire stimulates seed germination and facilitates establishment[63].

The hard seeded fire-responding taxa generally have thick testa which is scarified by the heat from fire. Brief heat shock induces imbibition by loosening cells in localized regions such as hilum chalazal cap, or strophiolar plug or possibly by denaturing inhibitors[5]. Heat shock might induce production of chemicals that cause changes in the seed coat or other external layers to overcome water impermeability barriers or that act as internal signals and mediate germination by induction of enzymes or growth regulators[64]. However, most of the rainforest seeds, especially those in the top few centimetres of soil were killed due to fire[28]. Repeated burning late in dry season kills most of the seedlings and saplings in dry African woodland[65]. Some species store seeds in the plant canopy in woody serotinous fruits, which delays the release of seeds until after a fire[66]. Other species produce and release seeds every year to build up a soil seed bank in the intervals between fires[67]. In still others the fire induces flowering and consequently augments the seed output[36]. There are species which show higher percentage germination when exposed to smoke[68].

Disturbance

There is increasing evidence that tree seedling population behaviour, i.e. recruitment, growth and survival in forests is influenced both by exogenous and endogenous disturbances[18,69]. Creation of microsites by uprooting of old trees significantly stimulates the recruitment of seedlings[70]. Disturbances which create gaps are known to play a major role in maintaining tree diversity in species-rich tropical forests. A study of 1200 gaps over a 13-year period in a tropical forest in Panama, indicated that gaps increased seedling establishment and sapling densities in a non-specific, broad-spectrum manner[71]. Recruitment limitation in such a situation explains the coexistence of a large number of species that have similar resource requirements and could lead to unlimited diversity. Higher seed production and seed weight in highly disturbed stands[72] could be attributed to enhanced resource availability[73]. Free-range grazing in dry tropical forest regions is disastrous to seedling recruitment of most species and it could potentially shift the composition of soil seed bank in favour of weedy grasses and forbs.

Ambient CO_2

Increase in atmospheric concentration of CO_2 would have significant impacts on various physiological and morphological traits of tree seedlings such as photosynthesis, water use efficiency, biomass, leaf area and allocation strategies[74,75]. Doubling of CO_2 concentration increased dry weight (1.3 to 4 times) and total leaf area (1.2 to 3 times) in seedlings among 15 tropical species[76,77].

Short-term and long-term exposure to elevated CO_2 may, however, influence seedling growth in different ways. While short-term elevated CO_2 stimulates seedling growth, long-term exposures may result in a small or no increase in seedling growth, because of the processes shown in Figure 2 (stipulated from refs 74 and 75). Growth under elevated CO_2 increased phenolics and tannins as well as toughness of the tissues in *Eucalyptus* species and the beetle, *Chrysophthartus flaveola*, which fed on this material did poorly[78].

Biotic variables

Seed size

Seed size is genetically determined and exhibits a wide intergeneric and interspecific variation. Various environmental factors that differ among habitats such as temperature, humidity, light, soil characteristics, dispersal syndromes, germination time, densities of competing plants, herbivore and fungi affect the production of and selection for different seed sizes. In the tropics, large seeds are associated with taller species[79], nutrient-impoverished sites[80] and an abundance of insects and pests[81]. Haig and Westoby[82] suggested that resource limitation did not increase the production of large seed size and that plants alter their seed number rather than seed mass. Among fruits within a plant, trade-offs between seed number and mass indicate the inability of the plant to provision all seeds equally well under resource-limited conditions[83]. Studies of trees in south-east Asia[84] and Australia[85] indicated that large seed size was associated with shade tolerance at the intergeneric level.

Large and heavy seeds contain a larger store of carbohydrates in the endosperm or cotyledons reflecting the availability of a larger source of energy to stimulate germination, seedling survival and growth, particularly in nutrient-impoverished and water-stressed soil, as the young seedlings from large-seeded species rely to a greater extent on nutrient support from the cotyledons than from the soil (see ref. 30 for review). The response of seedlings from different seed sizes to water stress may vary. For example, in *Albizia procera*, seedlings from large seeds had a higher biomass and leaf area and were more tolerant of long-term extreme water stress, while those from small seeds were more tolerant of moderate levels of water stress[56]. Large seed might provide energy for growth into higher light intensity strata and seedlings from large seeds may be able to cope better with temporary carbon deficits during early development which may arise from herbivory, predation, pathogenesis or from reduced photosynthesis due to temporary drought or shading[17]. A study of 31 moist deciduous broad-leaved trees led to the conclusion that large seeded species completed their shoot elongation and annual leaf production in a short period, irrespective of shading, whereas small seeded species attained maximum height (similar to those of large seeded species) only under open condition and had longer duration of leaf emergence, higher resource allocation to leaf production and rapid leaf turnover[86].

For certain rainforest species of Panama, there existed a negative correlation between seed size and abundance of seeds in the soil seed bank[87]. Small seeds have a better chance to enter into the soil easily than large seeds and therefore, would favour the build up of persistent soil seed bank, crucial for regeneration of species following disturbance[30]. On the other hand, 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. While examining the effects of

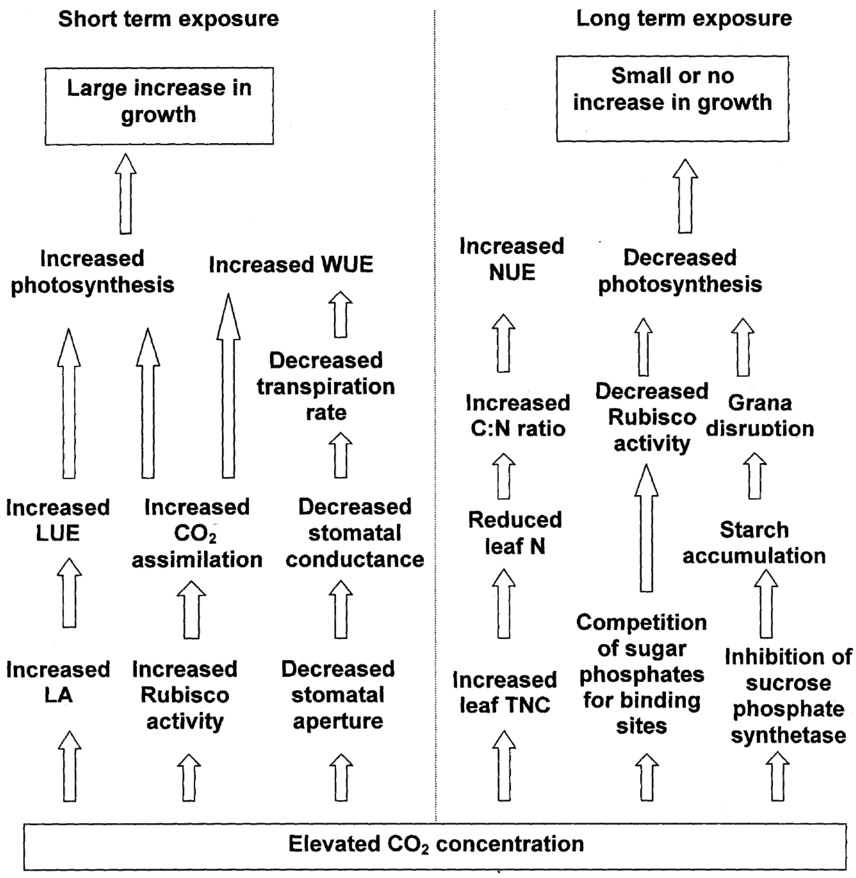

Figure 2. Major processes involved with the influence of short- and long-term exposures of seedlings to elevated CO_2. Short-term exposure to elevated CO_2 results in large increases in seedling growth due to increased leaf area (LA) and light use efficiency (LUE) and increased activity of Rubisco, which culminate into increased photosynthesis. At the same time a decrease in stomatal aperture and conductance results in increased water use efficiency (WUE). Long-term exposure, on the other hand, results into decreased photosynthesis through decreased activity of the Rubisco and grana disruption in the chloroplasts, culminating into small or no increase in seedling growth. In addition, increased total nonstructural carbohydrate (TNC) content of the leaf and reduced N concentration result in increased NUE.

seed mass on performance of seven sympatric rainforest woody species of Psychotoria, Paz *et al.*[88] suggested that seed mass did not have a general effect on emergence success and the effects of seed mass on seedling emergence were driven by external ecological factors more than by intrinsic effects of seed mass.

Seeds of several light demander rainforest trees such as some species of *Terminalia*, *Pterocarpus* and *Gosweilerodendron* are light and are dispersed by air current[89]. In wind, water and animal-dispersed species, the dispersal efficiency decreases with seed mass and there occurs a trade-off between seedling establishment and seed dispersal efficiency[90]. Variability in seed morphological and physiological traits within the same species of rainforest has been defined as intraspecific cryptic heteromorphism that arises probably due to environmental variability within and among trees during seed development and genetic conditioning[3]. Differential concentration of mineral nutrients in embryo and seed coat, irrespective of seed size could influence seedling establishment and growth[30].

Predators and parasites

Intense predation by beetles reduces seed production of the palm *Euterpe globosa* by more than 70% within one month of ripening, and only 1% of the original seed population ultimately produces seedlings[91]. Weevil damage in germinating seeds and seedlings of *Virola surinamensis*[92] and bruchid beetle damage in palm fruits[93] decreases with distance from mature trees. While studying post dispersal fate of seeds from a neotropical montane tree, *Ocotea endresiana*, Wenny[94] suggested that the germination occurred only in seeds regurgitated by birds, while seeds in intact fruits did not germinate at all. On the other hand, seeds removed by mammals showed complete inhibition of germination. Also, seeds of *Miconia affinis*, a neotropical rainforest species, began germinating sooner than control seeds when dropped by birds[45].

A large proportion of rainforest trees has seeds or fruits attractive to mammals and birds[89]. According to one estimate, 87–90% of the woody species in the high forest of Guianas are animal-dispersed[95]. Capability of seed dispersal and predation bestows upon mammals powerful roles in regeneration of tropical forests[96]. *Heteromys desmarestianus*, a small rodent, was responsible for removal of most of the seeds of *Astrocaryum maxicanum* and *Ampelocera hottlei* fruits in neotropical forests of Belize. These seeds were scatter-hoarded and protected from predation by other animals. Predation on green fruits or seeds may result in abortion of damaged fruits. A greater growth of remaining fruits compensates for this fruit loss[97].

Plant pathogens are an important cause of mortality for tropical seedlings, and their effect is aggravated in moist, heavily-shaded habitats[98]. Plant pathogens may thus represent an important source of selection against long periods of dormancy or quiscence in wet tropical seeds[17].

Mycorrhiza

Mycorrhizal association increases access of seedlings to nutrients and water and provides protection from root pathogens. It profoundly influences seedling survival and growth. Inoculation with *Scutellospora gilmorei* increased the height of plant *Euterpe oleracea* by 92%, stem diameter by 116% and dry matter production by 361% over uninoculated seedlings[99]. About 95% of the tree species occurring in tropical forests are purely endomycorrhizal, while ectomycorrhizals are only found in families Caesalpinaceae, Dipterocarpaceae, Myrtaceae, Pinaceae and some Euphorbiaceae[100]. *Glomus mosseae*-inoculated seedlings of *Casuarina equisetifolia* showed increased growth, nodulation and nitrogen fixation over uninoculated seedlings[101]. Significant increase in growth rate and biomass production was reported for seedlings of *Dendrocalamus strictus* inoculated with AM fungi[102]. Enhancement in seedling growth was maximum when *Acacia mangium*, *A. nilotica* and *Delonix regia* were inoculated with *Gigaspora margarita*, *A. leucophloea* with *Glomus fasciculatum* and *Derris indica* with *G. mossae*[103]. Endomycorrhizal inoculation[104] of *Dicorynia guianensis*, a rainforest tree species of French Guiana, increased seedling dry weight by 54–77%. Other species showing increase in plant growth after fungal inoculation are *Enterolobium cyclocarpus*, *Gmelina arborea*, *Acacia crassicarpa*[105], *Sesbania grandiflora*, *Albizia lebbeck*[106] and *Bambusa arudinacea*[107]. Mycorrhizae-inoculated N-fixers, such as *Anthyllis cistisoides*[108] and *C. equisetifolia*[109] have been successfully applied in restoration programmes.

Provenance

Populations of a species from different geographical locations (provenances) frequently show differential response due to genotype effect[30]. Seed traits (e.g. size and weight) of several tropical tree species such as *Acacia* spp[110], *Albizia lebbeck*[111] and *Leucaena leucocephala*[112] varied among provenances. Significant variation in germination traits among seed sources has also been reported for *Dalbergia sissoo*[113] and *A. nilotica*[114]. Provenances also show significant differences in post germination traits and growth performance of seedlings[30]. A study of 20 provenances of *D. sissoo* collected from different parts of India, indicated an inverse relationship between seed weight and rainfall, but a positive relationship between seed germination and rainfall, and between germination parameters and seedling growth parameters[115]. Other species showing such variations are *A. nilotica* (32 provenances from 5 countries)[116], *Eucalyptus camaldulensis* and *Acacia auriculiformis* (26 provenances from Australia and Papua New Guinea)[117]. Nitrogen fixing ability of seedlings of trees such as *Acacia albida* and *A. nilotica*, also varied when seeds were collected from different seed orchards. In a glasshouse study, Sun *et al.*[118] reported variation in growth and nodulation of seedlings among provenances, e.g. *A. mangium* (13 provenances), *A. auriculiformis* (4 provenances) and *Acacia melanoxylon* (2 provenances). Variation in chemical constituents in plant parts among geographical locations has been reported for *Acacia nilotica*[119], *Acacia* spp[120], *Prosopis cineraria*[121] and *A. lebbeck*[122].

Successional hierarchy, microsites and multiple cues

In a majority of studies discussed in the foregoing sections, the abiotic or biotic variables were considered in isolation, i.e. as single cues for germination or seedling establishment. In the field, a microsite often represents an interactive combination of variables. For example, high light condition is frequently associated with high temperature and low moisture. Further, large and small seeds, and those that have or have not passed through animal digestive systems may show quantitatively different responses to germination cues. A compilation of germination studies[123] on rainforest species of Puerto Rico showed a relationship between successional status and requirements for seed germination. Early successionals germinated at higher rates in high light, midsuccessionals in middle intensity light and late successionals in low light. Early successionals also required medium to high soil moisture, whereas late successionals germinated well under medium soil moisture. Further, late successionals showed a greater plasticity in their germination response compared to early successionals. A few species were independent of microsite, either germinating well or poorly everywhere. Therefore germination percentages recorded in germination chambers or seedling growth studied in a greenhouse under controlled conditions may have limited correspondence with the real-life situation of field microsites. Identifying multiple cues and germination niches through field-based studies, would permit manipulation of microclimatic conditions to maximize germination of desired native species and to suppress that of undesirable exotics.

Implications for India

India possesses almost the entire range of tropical forest, from dry deciduous to wet evergreen, yet surprisingly little field-based information exists on the ecological requirements at seed and seedling stages for the majority of individual or guilds of species, which could be translated into plans for conservation, enhancement and restoration of biological diversity. Systems of canopy manipulation and its timing with or without additional seed inputs, to suit seedling recruitment of species, particularly those depleting locally and those producing recalcitrant seeds, keeping in view the shade tolerance/intolerance syndrome for seedling growth as well as germination, need to be developed on the basis of specifically designed field experiments. Provision and retention of shade trees in appropriate numbers, rotational withdrawal of grazing, application of moisture conserving practices and development of site preparation techniques to curb competition from weedy grasses and forbs, are needed for areas preselected for biodiversity enhancement in dry tropical forests. Field studies are needed to determine the response of seeds and seedlings to periodic fire and to stresses of moisture and temperature in order to develop species/community-level plans for seedling recruitment in fire-prone and drought-affected forest areas. Information on the size and botanical composition of transient and persistent soil seed bank, and the extent and composition of local seed deposition need to be monitored for major forest types in order to be able to exploit this resource for the maintenance and enhancement of biological diversity. Integrated knowledge on seed size and longevity, dispersal syndrome, germination requirements, capacity of seedlings to tolerate moisture stress, shade dependence, appropriate mycorrhizal associations and suitable provenances for species which once established can further attract biodiversity, is crucial for region-specific restoration plans. Characterization of strains, identifying suitable plant–microbe combinations and development of inoculation techniques appropriate for field use are called for rhizobia, frankia and mycorrhizae-based restoration efforts. Responses of seedlings to nutrient amendment and to elevated CO_2 can be used to produce taller and heavier seedlings for transplantation on deforested and degraded lands, with a greater probability of success.

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1. Murphy, P. G. and Lugo, A. E., *Annu. Rev. Ecol. Syst.*, 1986, **17**, 67–88.
2. Singh, K. P. and Singh, J. S., *Int. J. Ecol. Environ. Sci.*, 1988, **14**, 31–45.
3. Vazquez-Yanes, C. and Orozco-Segovia, A., *Annu. Rev. Ecol. Syst.*, 1993, **24**, 69–88.
4. Rincon, E. and Huante, P., *Trees*, 1993, **7**, 202–207.
5. Bell, D. T., Plummer, J. A. and Taylor, S. K., *Bot. Rev.*, 1993, **76**, 24–73.
6. May, R. M., Lawton, J. H. and Stork, N. E., in *Extinction Rates* (eds Lawton, J. H. and May, R. M.), Oxford Univ. Press, Oxford, 1995, pp. 1–24.
7. Tilman, D., May, R. M., Lehman, C. L. and Nowak, M. A., *Nature*, 1994, **371**, 65.
8. Dobson, A. P., Bradshaw, A. D. and Baker, A. J. M., *Science*, 1997, **277**, 515–522.
9. Nepstad, D. C., Uhl, C., Pereira, C. A. and Cardoso da Silva, J. M., *Oikos*, 1996, **76**, 25–39.
10. Perfecto, I., Rice, R. A., Greenberg, R. and Van der Voort, M. E., *BioScience*, 1996, **46**, 598–608.
11. Nielson, K. and De Rosier, D., in *Monteverde: Ecology and Conservation of a Tropical Cloud Forest* (eds Nadkarni, N. and Wheel Wright, N.), Oxford Univ. Press, New York, 1999, p. 412.
12. Parotta, J. A., *J. Veg. Sci.*, 1995, **6**, 627–636.
13. Parotta, J. A., *Agric. Ecosyst. Environ.*, 1992, **41**, 115–133.
14. Ashton, P. M. S., Gamage, S., Gunatilleke, I. A. U. N. and Gunatilleke, C. V. S., *J. Appl. Ecol.*, 1997, **34**, 915–925.
15. Guariguata, M. R., Rheingans, R. and Montagnini, F., *Rest. Ecol.*, 1995, **3**, 252–260.
16. Guariguata, M. R., *Ecol. Appl.*, 2000, **10**, 145–154.
17. Foster, S. A., *Bot. Rev.*, 1986, **52**, 260–299.
18. Grubb, P. J., *Biol. Rev. Cambridge Philos. Soc.*, 1977, **52**, 312–335.
19. Janzen, D. H., *Evolution*, 1969, **23**, 1–27.
20. Mohamed-Yasseen, Y., Barringer, S. A., Splittstoesser, W. E. and Costanza, S., *Bot. Rev.*, 1994, **60**, 426–439.
21. Hilhorst, H. W. M. and Toorop, P. E., *Adv. Agron.*, 1997, **61**, 111–165.
22. Roberts, E. H., *Seed Sci. Technol.*, 1973, **1**, 499–514.
23. Whitmore, T. C., in *Tropical Trees as Living Systems* (eds Tomlinson, P. B. and Zimmerman, M. H.), Cambridge Univ. Press, 1978, pp. 639–655.
24. Hall, J. B. and Swaine, M. D., *The Distribution and Ecology of Vascular Plants in a Tropical Rain Forest: Forest Vegetation in Ghana*, Junk, The Hague, 1981, p. 383.
25. Yap, S. K., in *Tropical Ecology and Development 1* (ed. Furtado, J.), International Society for Tropical Ecology, Kuala Lumpur, West Malaysia, 1980, pp. 161–167.
26. Whitmore, T. C., *An Introduction to Tropical Rain Forest*, Clarendon Press, Oxford, 1990, p. 226.
27. Harper, J. L., *Population Biology of Plants*, Academic Press, London, 1977, p. 892.

28. Baskin, C. C. and Baskin, J. M., *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination*, Academic Press, San Diego, 1998, p. 666.
29. Willan, R. L., *A Guide to Forest Seed Handling with Special Reference to the Tropics*, FAO Forestry Paper, DANDIDA Seed Centre, Humleback, Denmark, 1985, p. 379.
30. Khurana, E. and Singh, J. S., *Environ. Conserv.*, 2001, 28 (in press).
31. Goor, A. Y. and Barney, C. W., *Forest Tree Planting in Arid Zones*, The Ronald Press Co, New York, 1976, p. 504.
32. Greaves, A., *For. Abstr.*, 1981, **42**, 237–258.
33. Bryndum, K., *Nat. Hist. Bull. Siam. Soc.*, 1966, **21**, 75–86.
34. Vazquez-Yanes, C. and Orozco-Segovia, A., in *Frugivores and Seed Dispersal* (eds Estrada, A. and Fleming, T. H.), Dr W. Junk, Dordrecht, 1986, pp. 71–77.
35. Plummer, J. A. and Bell, D. T., *Aust. J. Bot.*, 1995, **43**, 93–100.
36. Bell, D. T., Rokich, D. P., McChesney, C. J., Catherine, J. and Plummer, J. A., *J. Veg. Sci.*, 1995, **6**, 797–806.
37. Vazquez-Yanes, C. and Orozco-Segovia, A., *Oecologia*, 1990, **83**, 171–175.
38. Bliss, D. and Smith, H., *Plant Cell Environ.*, 1985, **8**, 475–483.
39. Fenner, M., in *Seed Development and Germination* (eds Kigel, J. and Galili, G.), Marcel Dekker, Inc., New York, 1995, pp. 507–528.
40. Walters, M. B. and Reich, P. B., *Ecology*, 1996, **77**, 841–853.
41. Reich, P. B., Tjoelker, M. G., Walters, M. B., Vanderklein, D. W. and Buschena, C., *Funct. Ecol.*, 1998, **12**, 327–328.
42. Reich, P. B., Walters, M. B. and Ellsworth, D. S., *Ecol. Monogr.*, 1992, **62**, 365–392.
43. Molofsky, J. and Fisher, B., *Ecology*, 1993, **74**, 261–265.
44. Kobe, R. K., *Ecology*, 1999, **80**, 187–201.
45. Elisson, A. M., Denslow, J. S., Loiselle, B. A. and Danilo, B. M., *Ecology*, 1993, **74**, 1733–1749.
46. Augsperger, C. K., *J. Ecol.*, 1984, **72**, 777–795.
47. Sasaki, S. and Mori, T., *Malay. For.*, 1981, **44**, 319–345.
48. Rao, P. B. and Singh, S. P., *Oecol. Planta.*, 1984, **6**, 161–166.
49. Ray, G. J. and Brown, B. J., *Rest. Ecol.*, 1995, **3**, 86–94.
50. Sah, V. K. and Singh, V., *Indian For.*, 1995, **121**, 273–275.
51. Some, L. M. and Kabore, H., Int. Symp. Forest Seed Problems in Africa, Harare, Zimbabwe, 1987, p. 334.
52. Teketay, D., *Trop. Ecol.*, 1998, **39**, 79–87.
53. Vazquez-Yanes, C. and Orozco-Segovia, A., *Physiol. Planta*, 1982, **56**, 295–298.
54. Maithani, G. P., Thapliyal, R. C., Bahuguna, V. K. and Sood, O. P., *Indian For.*, 1990, **116**, 577–580.
55. Fisher, B. L., Howe, H. F. and Wright, S. J., *Oecologia*, 1991, **86**, 292–297.
56. Khurana, E. and Singh, J. S., *Ann. Bot.*, 2000, **86**, 1185–1192.
57. Singh, J. S., Singh, K. P. and Jha, A. K. (eds), Final Technical Report, Ministry of Coal, Govt. of India, Dept. of Botany, Banaras Hindu University, Varanasi, 1996, p. 116.
58. Raaimakers, D. and Lambers, H., *New Phytol.*, 1996, **132**, 97–102.
59. Fernandes, M. F., Ruiz, H. A., Neves, J. C. L. and Muchovej, R. M. C., *Rev. Bras. Cienc. Solo*, 2000, **23**, 617–625.
60. Lewis, S. L. and Tanner, E. V. J., *Ecology*, 2000, **81**, 2525–2538.
61. Keeley, J. E., *Bot. Rev.*, 1991, **57**, 81–116.
62. Vazquez-Yanes, C., *Turrialba*, 1974, **24**, 176–179.
63. Champion, H. G. and Seth, S. K., *General Silviculture for India*, Govt. of India, Delhi, 1968, p. 511.
64. Keely, J. E. and Fotheringham, C. J., *Ecology*, 1998, **79**, 2320–2336.
65. Menaut, J. C., Lepage, M. and Abbadie, L., in *Seasonally Dry Tropical Forest* (eds Bullock, S. H., Mooney, H. A. and Medina, E.), Cambridge Univ. Press, Cambridge, 1995, pp. 64–92.
66. Lamont, B. B., Le Maitre, D. C., Cowling, R. M. and Enright, N. J., *Bot. Rev.*, 1991, **57**, 277–317.
67. Meney, K. A., Nielssen, G. M. and Dixon, K. W., *J. Veg. Sci.*, 1994, **5**, 5–12.
68. Dixon, K. W., Roche, S. and Pate, J. S., *Oecologia*, 1995, **101**, 185–192.
69. Brokaw, N. V. L., *J. Ecol.*, 1987, **75**, 9–19.
70. Petersson, C. J. and Pickett, S. T. A., *J. Veg. Sci.*, 1990, **1**, 657–662.
71. Hubbell, S. P. *et al.*, *Science*, 1999, **283**, 554–557.
72. Barik, S. K., Tripathi, R. S., Pandey, H. N. and Rao, P., *J. Appl. Ecol.*, 1996, **33**, 1551–1560.
73. Waring, R. H., in *Comparative Analysis of Ecosystems* (eds Cale, J., Lovett, G. and Findlay, S.), Springer-Verlag, New York, 1991, pp. 222–238.
74. Baker, J. T. and Allen Jr. L. H., *Environ. Pollut.*, 1994, **83**, 223–225.
75. Drake, B. G., Gonzalez-Meler, M. A. and Long, S. P., *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 1997, **48**, 609–639.
76. Devakumar, A. S., Udayakumar, M. and Prasad, T. G., *Curr. Sci.*, 1996, **71**, 469–472.
77. Devakumar, A. S., Sesha Shayee, M. S., Udayakumar, M. and Prasad, T. G., *J. Biosci.*, 1998, **23**, 33–36.
78. Lawler, I. R., Foley, W. J., Woodrow, I. E. and Cork, S. J., *Oecologia*, 1997, **109**, 59–68.
79. Grubb, P. J., *New Phytol.*, 1998, **138**, 169–170.
80. Milberg, P., Perez-Fernandez, M. A. and Lamont, B. B., *J. Ecol.*, 1998, **86**, 624–632.
81. Coley, P. D. and Aide, T. M., in *Herbivory: Tropical and Temperate Perspectives* (eds Price, P. W. *et al.*), John Wiley, New York, 1991, pp. 25–49.
82. Haig, D. and Westoby, M., in *Plant Reproduction Ecology: Patterns and Strategies* (eds Lovett Doust, J. and Lovett Doust, L.), Oxford Univ. Press, New York, 1988, pp. 60–79.
83. Mehlman, D. W., *Am. J. Bot.*, 1993, **80**, 735–742.
84. Metcalfe, D. J. and Grubb, P. J., *Can. J. Bot.*, 1995, **73**, 817–826.
85. Grubb, P. J. and Metcalfe, D. J., *Funct. Ecol.*, 1996, **10**, 512–520.
86. Seiwa, K. and Kikuzawa, K., *Can. J. Bot.*, 1991, **69**, 532–538.
87. Dalling, J. W., Hubbell, S. P. and Silvera, K., *J. Ecol.*, 1998, **86**, 674–689.
88. Paz, H., Mazer, S. J. and Martinez-Ramos, M., *Ecology*, 1999, **80**, 1594–1606.
89. Richards, P. W., *The Tropical Rain Forest: An Ecological Study*, Cambridge Univ. Press, Cambridge, 1996, p. 575.
90. Ganeshaiah, K. N. and Uma Shaanker, R., *Oikos*, 1991, **60**, 3–6.
91. Van Valen, L., *Biotropica*, 1975, **7**, 260–269.
92. Howe, H. F., Schupp, E. W. and Westley, L. C., *Ecology*, 1985, **66**, 781–791.
93. Wright, S. J., *Ecology*, 1983, **64**, 1016–1021.
94. Wenny, D. G., *Ecol. Monogr.*, 2000, **70**, 331–351.
95. van Roosmalen, M. G. M., *Fruits of the Guianan Flora*, Inst. Syst. Bot, Utrecht, 1985.
96. Brewer, S. W. and Rejmanek, M., *J. Veg. Sci.*, 1999, **10**, 165–174.
97. Kozlowski, T. T. and Keller, T., *Bot. Rev.*, 1966, **32**, 293–382.
98. Augsperger, C. K. and Kelly, C. K., *Oecologia*, 1984, **61**, 211–217.
99. Chu, E. Y., *Pesqui. Agropecu. Bras.*, 1999, **34**, 1019–1024.
100. Redhead, J. F., in *Tropical Mycorrhiza Research* (ed. Mikola, P.), Clarendon Press, Oxford, 1980, pp. 127–142.
101. Diem, H. G. and Gauthier, D., *C. R. Seances Acad. Sci. Paris Ser. 3*, 1982, **294**, 215–218.
102. Ravikumar, R., Ananthakrishnan, G., Appasamy, T. and Ganapathi, A., *For. Ecol. Manage.*, 1997, **98**, 205–208.

103. Selvaraj, M., Syamala, D., Arumugam, S. and Rao, M. V., *Indian For.*, 1996, **122**, 1161–1167.
104. Bereau, M., Loisanna, E. and Garbaye, J., *Ann. Sci. For.*, 1997, **54**, 271–277.
105. Pramono, I. B. and Siregar, C. A., *Bull. Penelitian Kehutanan-Pematang Siantar*, 1999, **15**, 153–163.
106. Kumar, P. P., Reddy, S. R. and Reddy, S. M., *J. Mycol. Plant Pathol.*, 1999, **29**, 385–388.
107. Paroha, S., Chandra, K. K. and Bhandari, P. S., *Vaniki Sandesh*, 1999, **23**, 21–23.
108. Requena, N., Jeffries, P. and Barea, J. M., *Appl. Environ. Microbiol.*, 1996, **62**, 842–847.
109. Wood, C. V., *Trees for Wastelands*, Mombasa Baobab Farm Ltd. Bamburi, 1987.
110. Bagchi, S. K., Joshi, D. N. and Rawat, D. S., *Silvae Genet.*, 1990, **39**, 107–110.
111. Kumar, N. and Toky, O. P., *Nitrogen Fixing Tree Res. Rep.*, 1993, **11**, 64–67.
112. Hooda, M. S. and Bahadur, R., *Seed Res.*, 1993, **21**, 46–51.
113. Vakshasaya, R. D., Rajora, O. P. and Rawat, M. S., *For. Ecol. Manage.*, 1992, **48**, 265–275.
114. Ginwal, H. S., Gera, M. and Srivastava, R. L., *Range Manage. Agrofor.*, 1994, **15**, 187–197.
115. Gera, M., Ph D thesis, Guru Ghasidas University, Bilaspur, MP, 2000.
116. Ginwal, H. S., Gera, M. and Srivastava, R. L., *Ann. For.*, 1995, **3**, 35–44.
117. Yang, M. Q. and Zeng, Y. T., Proceedings of an International Workshop, Bangkok, Thailand, 11–15 February, 1991.
118. Sun, J. S., Sands, R. and Simpson, R. J., *For. Ecol. Manage.*, 1992, **55**, 209–223.
119. Bagchi, S. K. and Singh, J., *Indian For.*, 1994, **120**, 529–532.
120. Babu, R. C., Natrajarathnam, G., Padmanabhan, B. and Dharmraj, G., *Indian J. For.*, 1987, **10**, 276–278.
121. Arya, S., Bisht, R. P., Tomar, R., Toky, O. P. and Harris, P. J. C., *Agrofor. Syst.*, 1995, **29**, 1–7.
122. Kumar, N. and Toky, O. P., *Agrofor. Syst.*, 1994, **25**, 217–225.
123. Myster, R. W. and Everham III, E. M., *Trop. Ecol.*, 1999, **40**, 89–98.

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