

# PATTERNS OF SEED LONGEVITY AND GERMINATION IN THE TROPICAL RAINFOREST

*C. Vázquez-Yanes and A. Orozco-Segovia*

Centro de Ecología, UNAM. Apartado 70-275, Ciudad Universitaria, 04510,  
México

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## *Abstract*

Tropical rainforest plants produce seeds showing a wide range of sizes, shapes, structures, chemical composition, water content, dormancy mechanisms, and patterns of longevity. Prompt germination seems to be the most common behavior, although there are many cases where germination is delayed by a hard coat or endogenous or enforced dormancy mechanisms. Some gap colonizers show sophisticated light or temperature regulated dormancy. Most rainforest seeds remain alive for a short time in the soil, even those that form part of the soil seed bank.

## INTRODUCTION

Knowledge of seed biology is essential to understanding community processes like plant establishment, succession, and natural regeneration. Thus, it is one of the basic tools for plant population management. For the tropical rainforest, information on seed physiology and ecology is still scarce and dispersed. Some aspects of this matter such as seed ecophysiology, response to gaps, characteristics of dormancy and longevity mechanisms, structure of soil seed banks, significance of seed size, and the role of seed in succession and management have been reviewed recently (35, 39, 51, 116, 119, 122, 126).

Scant information is available on the longevity of seeds in the forest or in

storage, their dormancy mechanisms, the display of their germination in the field, and the effects of environmental factors on seed behavior. This information nevertheless reveals some of the principal characteristics of longevity and germination patterns for the seeds of major ecological groups of woody plants, uncovering also some of the environmental constraints that may have selected certain seed longevity and germination patterns within each group. One cannot ignore, however, the fact that seeds of tropical rainforest plants, as those of any other plant community, may possess an assembly of morphological and physiological features that may, in part, reflect responses to selective pressures in the environment or in past environments where the plants evolved. Alternatively, they may be a random collection of traits without adaptive meaning, resulting either from phylogenetic lineage effects and/or from the structure of reproductive organs developing under the effect of changing environments. This mixture of adaptive and neutral characteristics in the seeds complicates the description of distinctive features of seed behavior in the tropical rainforest.

## PATTERNS OF ECOLOGICAL LONGEVITY

Ecological longevity of seeds is the mean duration of dormancy in natural conditions: the mean interval elapsing between seed maturation and dissemination, and seed germination or death in the soil, whereas potential longevity is the maximum duration of germination capacity (viability) of dormant seeds in optimal storage conditions (13, 27).

Seeds play four important roles in the persistence of the species populations, although not all of them are equally important in different groups of plants. They have been modulated by prevailing environmental conditions in each community, in interaction with the distinctive life history traits of the plant populations. The four roles are: reproduction, dispersal within the same community, expansion to new territories or other habitats, and survival of the germplasm through seasons or environmental conditions unfavorable for growth (27).

The constantly high temperatures and predominantly moist environment of the rainforest have selected seed traits achieving mainly reproductive and dispersal functions. The preservation of living germplasm through periods characterized by adverse environmental conditions for the successful establishment of new individuals seems to be less important for the perpetuation of rainforest plants than plants in more seasonal ecosystems. In fact, most rainforest species of seeds, at the localities where they have been studied, tend to germinate fast and simultaneously after dissemination, lacking any period of dormancy in the soil. Most of these seeds, when released, have a high moisture content and an active metabolism, expressed through an

uninterrupted respiration rate during the period of quiescence between seed maturation and germination (34, 35, 40, 42, 43, 93, 103, 105, 119). Some mechanisms involved in generating the capacity of the seeds to remain alive and dormant for some time are linked to the level of basic metabolic activity and the amount of free water left in seed cells during quiescence. Tropical forest seeds keep other cellular functions active, such as synthesis of macromolecules (38, 73–76). A seed showing a continuous and uninterrupted respiratory rate would exhaust energetic reserves very fast, eventually preventing germination in the soil (67). In some cases photosynthesis is already present in the cotyledons of the embryo (56), and some species may even exhibit uninterrupted development of the embryo in the seed until a seedling is formed and disseminated. This phenomenon is perceived as a sort of plant viviparity (58, 116).

The mean ecological longevity of seeds in the tropical rainforest may be one of the shortest of any plant community (35, 39, 60, 63), because seeds tend to germinate soon after dispersal. Otherwise they are quickly killed in a soil environment characterized by continuously high moisture and temperature, which allows the permanent activity of diverse populations of predators and parasites (35, 97). Growing seedlings are often less vulnerable to parasitism and predation than are dormant seeds. In *Dyera costulata* from Malaysia, only quiescent seeds are thoroughly eaten by ants. When the cotyledons become green and germination starts, ants end their attacks (25).

Not every rainforest seed is equally susceptible to these deleterious factors in the environment. Many plants produce seeds with a hard insulating seed coat. Sometimes this anatomical barrier is impermeable to water and/or oxygen, interfering with fast hydration or respiration. It thus delays the development of appropriate conditions for the onset of metabolic activity after the seed reaches the soil, until the coat becomes permeable through weathering and microbial deterioration (10). These seeds are characteristic of some leguminous, bombacaceous, and malvaceous trees, among other families. The longest living tropical seeds at above freezing temperatures (macrobiotic) are those having impermeable hard coats (46). For example, seeds of the balsa tree, *Ochroma lagopus*, from tropical America, taken from herbarium specimens, remained viable for 44 years (70).

A few authors have buried seeds in mesh bags or other kinds of confinements in the soil of the rainforest, in an attempt to obtain a more precise evaluation of seed longevity in the natural environment, under conditions that exclude most seed predators that cannot penetrate the confinement. All these experiments indicate that only species of plants that produce seeds with an enforced dormancy mechanism, such as light or temperature requirement, remain dormant. Alternatively, seeds with a hard coat may survive burial for a considerable period. Some of the species found dormant,

sometimes for more than a year, belong to the genera *Acacia*, *Cecropia*, *Piper*, and *Trema*, among others (47, 48, 84, 88).

Ecological evaluations of the longevity of seeds undergoing natural dissemination and persistence in the tropical rainforest soil are scarce. Seeds of many species remain in the soil little more than a week, as does *Virola surinamensis* (105), or nearly two months, as does *Omphalea oleifera* (62), both species from tropical America. In contrast, some pioneer tree seeds show a relatively longer ecological longevity: seed rain, soil seed bank, and seed predation were evaluated in *Cecropia obtusifolia* from Mexico. The calculated turnover rate of these seeds in the soil seed bank was 1.02 to 1.07 years (5).

Although brief longevity combined with fast germination after dispersal is probably the most common feature of tropical rainforest seeds, many species do show delayed germination after dispersal. This behavior has been found in a number of seed germination observations performed at the community level (38, 62, 80). It is also common to find an extended germination period within the same seed cohort. Finally, in many rainforests there is a persistent soil seed bank dominated by the dormant seeds of a small fraction of the species present in the community (39, 126). These facts indicate that a number of endogenous and external factors may be implicated in the endurance by seeds of the deleterious forest soil environment. The factors that independently or in combination may extend ecological longevity in the forest soil are: (i) the presence of a dormancy mechanism that prevents fast germination, allowing seeds to be buried by litter or soil shortly after dissemination (48), (ii) interruption of respiratory metabolism and other cellular functions of seeds (40), (iii) the presence of a hard and/or impermeable coat that prevents fast rehydration of the seeds and diminish predation (23, 93), (iv) abundant seed production that may allow some seeds to survive the attacks of parasites and predators (5), and (v) the presence of strong chemical defenses in the seeds against parasitism and predation (31, 52).

## PATTERNS OF SEED GERMINATION

The great botanical diversity of the rainforest is reflected in a wide range of possibilities in the expression of the development of seed germination, ranging from seeds that are disseminated already germinated to those provided with different types of enforced dormancies, a characteristic of the permanent seed banks of most tropical forests (39, 126).

Some of the structural factors involved in the postponement of germination in the seeds are: level of residual moisture in the seed at maturity, the presence of a hard coat, the size and stage of development of the embryo, and the distribution of reserves in the seed tissues. The physiological factors include permeability to water and oxygen, balance of growth factors in the embryo,

speed of mobilization of seed reserves to the embryo, and the presence of specific environmental requirements to start germination. The information available about many of these aspects of seed biology for rainforest seeds is extremely scarce and has been obtained mainly from experiments in laboratory or nursery conditions. Additionally, the display of germination as epigeal, hypogeal, and intermediate forms may have some connection with the speed of germination. Epigeal germination is usually fast and synchronous (79); on the other hand, cryptocotylar species often show retarded germination (24, 32), although there are exceptions (29, 32).

### *Prompt Germination*

The following examples of germination exhibit a period of quiescence between the end of seed maturation within the fruit and the emergence of the embryo from the seed coat. The seeds of a large number of studied species tend to germinate very fast soon after arrival on the ground. *Symphonia globulifera* from South America is an example of this: in the presence of water and at the temperatures prevailing in the forest, the radicle of the seeds of this species protrude from the coat very soon, and less than a month after sowing, viable seeds are fully germinated (17). Lower temperatures may delay this process. These seeds have an average moisture content of about 67%, though different tissues of the seeds may have different moisture levels.

Many tropical rainforest seeds have a high moisture content (35 to 65%, or more) (119); however, the embryo reaches the full turgor required for cell elongation only in the moist soil of the forest where germination starts immediately. This type of germination behavior has been observed also in field studies (2, 7, 34, 38, 53, 57, 80, 92, 97). About 65% of 330 Malaysian trees showed fast germination after dispersal to the soil surface (80). Species that behave in this manner are often very sensitive to dehydration and would lose their viability if they are dried or heated by direct insolation when falling in open places (20, 21, 65, 66, 95). The simultaneous emergence of seedlings produced by prompt germination explains the even-aged populations of seedlings often observed during the rainy season in many tropical forests (41, 61).

There are seeds that can tolerate some degree of dryness when lying in the soil; among them germination often is delayed until there is an increase in soil moisture. Some examples are found in the literature about this type of behavior. The seeds involved often have relatively lower moisture content or greater water retention capacity because of seed size or high lipid content (95, 105). More rarely other factors involved in this behavior, such as the presence of protective layers of tissues from the fruit, have been reported (64, 66).

Some studies indicate that seed germination in some seasonal rainforests peaks soon after the beginning of the rainy season (26, 38, 57). The tropical

American cedar *Cedrela odorata* and the American mahogany *Swietenia macrophylla* (4, 22) are good examples of wind-dispersed seeds released with low moisture content, for which the main limit on fast germination is water availability. These species may remain in the soil in a quiescent state and then germinate readily as soon as the environment becomes moist. In Mexico, experiments including the artificial irrigation of forest soil before the rainy season induced germination in seeds of *C. odorata* and *Brosimum alicastrum* lying dormant in the soil (14).

Because germination of forest seeds often takes place on the soil surface, the balance between moisture gains from the ground and losses by transpiration determines the moment at which the seed is moist enough to start germinating. This factor may be one of the causes of the spread of germination over time within a seed cohort, a frequent phenomenon among seeds germinating in the field. In some cases, seeds need to be covered by litter or partially buried in order to germinate (12, 100). These conditions may produce an improvement in the hydraulic balance between the soil and the seed, eventually bringing about full turgor in the embryo.

### *Delayed Germination*

A waiting period before the beginning of germination, unrelated to the moisture balance between seeds and environment, when the seeds lie in the soil, is also fairly common among tropical rainforest plants (116). Of numerous plants studied in Malaysia (80), 35% started germination more than 20 weeks after sowing. In Costa Rica, the seeds of *Dendropanax arboreus* germinated 11 weeks after sowing, and those of *Miquartia guianensis* and *Xilopia xericophylla* required 21 weeks to start germination (42). Some seed cohorts not only germinate long after sowing but also show an extended germination period in the forest. For example, *Caryota mitis* from Malaysia needs 29 weeks to begin germination and takes another 14.5 weeks to complete it (92). *Astrocaryum mexicanum* starts germination after 32 weeks (62).

In some cases delayed germination may be due to limited permeability of the seeds to water and oxygen. Alternatively it may be attributed to the existence of an endogenous dormancy due, among other factors, to immaturity of the embryo or to an inadequate balance of growth factors like hormones, e. g. the presence of abscisic acid and/or the absence of gibberellin (13). Virtually nothing is known about these types of obstacles to germination and related processes in rainforest seeds. However, some experiments appear to indicate that processes comparable to the after-ripening characteristic of many temperate trees may be found among some tropical trees, and that sometimes germination can be accelerated with hormones like gibberellic acid or even by cold storage (55, 72, 88, 93, 113, 114).

Studies of groups of species from different regions indicate that very often delay in germination is heterogeneous within the same seed cohort. This produces a flux of germinating seeds that may last for weeks or months, as in *Euterpe globosa* from Puerto Rico (9). This peculiar behavior may be due to intraspecific differences in permeability or to the duration of endogenous mechanisms of dormancy. There are many cases of seed populations where the time from the beginning to the end of germination is long (11, 42, 77, 78, 80, 81, 89). The flux of germinating seeds may develop in several ways. For example, germination of seeds may be continuous over a period of weeks or months, as in the case of *Nectandra ambigens* (119). Intermittent germination produced irregularly over a period of weeks or months, as in *Rheedia edulis* (95). Both of these examples are from Mexico. In the Brazilian tree *Psidium acutangulum*, a bimodal germination period has been observed at 30 and 70 days after the seeds were sown in three different kinds of soil (28). There are cases where most seeds germinate fast and a fraction of the seed sample remains dormant for a long time before germinating gradually, as in *Nauclea maingayi* from Malaysia (81). Finally, periodic germination occurs regularly during favorable conditions between two fruiting seasons in *Heliocarpus appendiculatus* from Mexico (96).

Population variability in the timing of seed germination may be due to the intraspecific cryptic heteromorphism often shown by rainforest seeds (defined as a continuous variability in seed morphological and physiological traits within the same species). This heteromorphism is probably due either to environmental variability within and among trees during seed development or to genetic conditioning. Variability has been measured in various species in features such as: seed size, weight, moisture content, viability and speed of germination in relation to temperature (1, 22, 26, 53, 54, 89, 104). Populations of widely distributed species may show significant geographical variability among seed provenances in germination responses, including responses to different temperatures (129).

Seeds that remain dormant for a period in the soil may develop a new environmental requirement for germination; this is known as induced or secondary dormancy. This type of dormancy has been well documented in temperate regions, but little is known about it in the rainforest. A possible case is represented by *Adenanthera pavonina* from Malaysia, whose freshly collected seeds started germination soon after being sown, but whose seeds stored in the laboratory required six months after sowing to begin germination (37). In photoblastic seeds of different species buried for known periods of time, the germination responses fluctuated widely with time after the exhumation of the seeds from the soil, suggesting the consecutive development and disappearance of a secondary dormancy (84, 88). These kinds of responses are often found in buried seeds of temperate weeds that develop cyclic

secondary dormancy. When buried, with time, photoblastic seeds lose sensitivity to light, but they may remain dormant in the soil under the effect of a secondary dormancy developed in the soil. Some evidence of this change of dormancy mechanism has been found in *Piper*, spp. but more detailed studies are required (84).

**GERMINATION DELAYED BY A HARD COAT** Many rainforest plants produce seeds with an impermeable coat that prevents prompt germination. In the forest soil these seeds gradually become permeable under the effect of microorganisms that degrade the coat, with natural temperature alternations in gaps or with weathering. This kind of dormancy spreads germination of a seed cohort over a wide interval, according to the rate at which the seed coats become permeable, and so it improves the chance of some seedlings surviving through time. The presence of a hard coat rendered permeable over time, combined with heteromorphism in coat hardness or degree of impermeability among seeds, may prolong the germination period of seeds (29, 30, 33). For example, in *Adenanthera pavonina*, germination started from the first day of sowing in a nursery and continued until more than a year later when full germination was reached (37, 81). A similar behavior has been observed in various species from different regions (7, 11, 30, 33, 80, 130). Some species may have a hard coat-imposed dormancy combined with some kind of endogenous dormancy, both of which prevent germination for some time after the elimination of the coat impediment, as in *Maesopsis eminii* from Africa (71).

The coats of these seeds become permeable through the action of moist and dry heat, strong acids, coat erosion or piercing, or sometimes transit through animal guts (8, 29, 30, 71, 98, 110, 111, 124, and many others). Often, transit through the gut of animals has been referred to as one of the principal factors triggering seed germination among animal-dispersed seeds. However, several studies indicate that there is often little difference between responses of seeds taken directly from the fruits and those taken from the feces of animals (59, 117).

There are some cases of germination enhancement among species of seeds either with hard coats or provided with soluble chemical inhibitors for germination, or in species having hard indehiscent fruits, but examples for the rainforest are hard to find. Nevertheless, the germination of seeds lying in animal feces may be enhanced by the temperature or moisture of this substrate, which makes feces a suitable nursery for seedling development (3, 49). Transit through animal guts may also increase the speed of germination, probably due to gut temperature and an increase in seed moisture content (68). Sometimes transit through guts of animals with long-lasting digestive processes can damage the seeds (117).



## ENVIRONMENTALLY REGULATED GERMINATION

The prevailing temperatures and light conditions in the tropical rainforest throughout the year are adequate for the immediate germination of most seeds. However, some plants produce seeds with an environmental sensor that delays germination until specific conditions of light and temperature occur in the environment. This regulation of germination by temperature alternations, light quality, or a combination of both is common among plants participating in the early colonization of gaps (116, 126). The environmental sensors of these seeds detect changes in their surroundings that correspond to the arrival of favorable conditions for germination and establishment. In dense forests, the initiation of a wider temperature alternation in the soil and changes in the photon flux density and quality of the light arriving at the ground are signals of canopy destruction, and/or disappearance of litter layer, and/or exhumation of seeds produced by soil disturbance (90, 91, 122).

In nature, enforced dormancy is most frequent in opportunistic invader weeds, either among ruderals from disturbed places or in crop weeds. It is much less frequent among primary forest trees of any kind. Nevertheless, some cases of enforced dormancies have been found in tropical forest plants.

A study of the survival of 50 Australian rainforest species of seeds buried in forest soil inside nylon bags indicated that pioneer and early secondary plants survived longer. On the other hand, soft-coated seeds of primary forest trees did not develop any kind of dormancy (48). The heliophile pioneer woody species are often the most abundant components of the soil seed bank (39, 116, 119, 122, 126).

To identify the existence of an environmentally enforced dormancy, specific treatments and germination conditions are required. Seeds with this kind of dormancy germinate readily soon after dispersal either in the presence of direct sunlight or in shade produced by other materials different from green canopies, under normal temperature fluctuations. Germination beneath neutral shade can give the impression that the seeds lack dormancy (122).

Rainforest seeds with an enforced dormancy requiring light for germination may remain dormant for a long time in darkness, if sown on a moist surface in laboratory conditions at temperatures suitable for germination. They germinate quickly as soon as light is provided, and they demonstrate high viability (85).

### *Temperature-Regulated Germination*

The induction of germination in seeds requiring temperature alternations may be due to a coat rendered permeable by heat, to an effect of the temperature on internal enzymatic kinetics that allows changes in the biochemistry of the

seed cells which trigger germination, or to the permeability of the cell membrane of the embryo (45).

Many seeds with an impermeable coat have a suberized layer either in the coat sclerenchyma or at the micropyle. Heat may melt this layer, allowing water to penetrate the seed. Some seeds require temperatures no higher than 45°C to become permeable to water. This can easily occur at the bare soil surface during a sunny day (115).

Fires have been found to have an important effect on the demise or, contrarily, on the germination of seeds lying in recently deforested soils (18, 106). The gap tree *Ochroma lagopus* has a suberized clear line in the palisade sclerenchyma of the seed coat that becomes permeable following heating of the soil by superficial fires or by induction of marked alternations in temperature produced by direct insolation of the soil surface (111, 124).

The sudden establishment of a soil temperature fluctuation regime characteristic of many gaps is also a cue for germination in seeds lacking a hard seed coat. The internal sensor for this change in environmental conditions has been related to the kinetics of certain enzymes or to the permeability of the cell membrane of the embryo (45). A pioneer tree from Mexico, *Heliocarpus donnell-smithii*, requires more than 10°C of daily temperature alternation for full germination (115).

### *Light-Regulated Germination*

The plant pigment phytochrome is the physiological sensor of light in seeds. Light-controlled seed germination has been associated with this pigment since the pioneer studies on lettuce seed (16).

Phytochrome exists in two main forms that are interconvertible by exposure to different light qualities (wavelengths). The active (germination-inducing) form, called Pfr, is converted from the inactive form Pr by exposure to red light (R, between 655 and 665 nm). Far-redlight (FR, 725-735 nm) converts Pfr to Pr, often reversing the effect to red exposure. Seeds disseminated with Pr need a light stimulus of the proper R/FR ratio such as sunlight after seed imbibition for germination. Otherwise they remain dormant for variable periods, sometimes for years (47). Seeds may also be disseminated with enough Pfr for dark germination, but they may later acquire a light requirement after burial or just after exposure to low R/FR ratio light on the soil surface under a canopy (108).

Seeds requiring light for germination are called positive photoblastic seeds. Positive photoblasticity has essentially two ecological roles: the preservation of dormancy of buried seeds, and the preservation of seeds of heliophytes dispersed to shaded sites (120). Photoblastic species differ in their sensitivity to a particular Pfr/Pt (active phytochrome/total phytochrome) photoequilibrium established by a given R/FR ratio (99). Some seeds may germinate under

light with a very low R/FR ratio but not in darkness, indicating that the Pfr/Pt required to trigger germination can be attained beneath green canopies but not in the darkness produced by deep soil burial (109, 120).

Seeds beneath green canopies or in litter may still receive enough light to promote germination; thus it seems that only extremely low photon flux densities are required for phytochrome-mediated light sensitivity. For example, *Cecropia obtusifolia* can be stimulated to 80% germination by exposure to light of only  $0.026 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  buried in soil at a depth of 4 mm (15). In this case, the factor inhibiting germination under canopies is light quality, because light penetrating through green foliage or litter is enriched in Fr relative to R. Sunlight has a mean R/FR ratio of 1.2, but beneath green canopies the ratio may be reduced to levels below 0.5 (123). There are examples of the germination-inhibiting effect of the light filtered by green canopies and green leaves in plants from tropical rainforests (6, 53, 84, 92, 107, 112, 125).

During gap formation, the light environment affecting light-mediated seed germination may change in three ways. First, deeply buried seeds may be exhumed by the uprooting of plants; second, smaller soil disturbance may expose seeds to more light; and third, disturbances of canopy, litter, or both may drastically alter the R/FR ratio of the light reaching the soil surface (122). One of the characteristics of phytochrome mediated germination is its photoreversibility within certain specific time limits. The ecological consequences of this phenomenon may be related to detection of true light gaps as opposed to sunflecks (84, 86, 118, 120). Sunfleck incidence on a given soil patch is brief and unpredictable, depending on canopy structure, weather, season, and orientation (19).

The frequency of sunflecks creates heterogeneous environments for germination of photoblastic seeds inside the forest, determining the amount of seeds that will germinate or remain dormant in each place. Inside the forest there is a light mosaic on the ground which is not adequate for germination of some of the photoblastic seeds, because the R/FR ratio of the light required for their germination is relatively high (83, 84).

Conversely, sunlight occurs more predictably in gaps, where it lasts for longer periods of time (123). *Cecropia obtusifolia* requires hours of light with a high R/FR ratio for germination (125). In species of *Piper* with contrasting habitats in the forest, each one required a different light quality and quantity for germination. Some germinated in low R/FR ratio inside the forest whereas others required long periods of light of high R/FR ratio outside the forest for germination (84).

Dispersal by animals may alter seed dormancy because of the chemical and physical environment in animal guts during the transit of seeds through them. One simple change during endozoochory dispersal is the increased moisture

content that the seeds acquire. Experiments performed with *C. obtusifolia* seeds indicate that the short transit period in bat intestines is less deleterious than the longer passage through monkey intestines. This passage may alter the optical properties of the seed coat and therefore the photoblastic response (117).

Seed water content when the seed is dispersed to the soil surface affects the R/FR ratio required to induce germination. Preimbibed seeds of *Piper auritum* in a Mexican rainforest germinated at lower R/FR ratios than dry seeds. Possibly phytochrome sensitivity depends on the degree of hydration when the seed is first exposed to the forest light environment, because of an increased sensitivity of phytochrome to FR in dry as compared to moist seeds (82).

Both light sensitivity and photoreversion timing allow the seeds of gap pioneers to remain dormant for a period after arrival in the community. Afterwards, seeds may gradually change their physiological properties and germinate or, alternatively, remain dormant under the control effect of a different set of factors such as light quality and quantity beneath the litter or beneath a soil layer, or chemical characteristics of the soil such as partial anaerobiosis. Thus, some originally dormant seeds under an undisturbed canopy may germinate in the shade after some time or as a consequence of litter and/or soil disturbance alone (P. Grubb, personal communication).

Only a few experiments on light sensitivity have been performed with seeds coming from soil storage. Experiments with *Piper* species in a Mexican rainforest, in which imbibed seeds were buried for up to one year before testing for germination, showed that the light requirements for germination changed in different ways through time for different species. Seeds may become either more sensitive or indifferent to light, or they may change in the response to the R/FR ratio (84, 117).

The quality of light in the environment where the infructescences *P. auritum* ripened had an effect on the balance of phytochrome in the seeds and therefore may have affected the sensitivity of the seeds to light, creating an intraspecific heteromorphism in the germination responses of the seeds to different light environments (82).

Photoblastism has also been found among other rainforest plants such as strangler trees (102), some understory shrubs (84), and spores of ferns (87).

### *Interactions of Light and Temperature*

The clearing of vegetation leads to greater fluctuation of soil surface temperatures because of direct insolation. These temperature fluctuations may change the response to the light stimulus and affect the speed of germination by shortening the period of illumination required, as shown for the Mexican pioneer *Urera caracasana* (86). Some seeds that are dormant in darkness or

in low R/FR ratios of light at constant temperature may germinate in those conditions under a fluctuating temperature regime. For example *C. obtusifolia* showed partial germination in darkness under an alternating temperature regime of 20–30°C. Most seed samples of this species did not germinate at a constant temperature without light (120).

### *Effect of Litter on Germination*

The layer of litter on the forest floor is an important element controlling germination, because it may be either inhibitory or stimulating. Litter may act as a nursery which holds enough moisture for the germination of large seeds (44, 65, 69, 97). Alternatively, litter can become a physical barrier for the emergence of seedlings derived from small seeds that lack the reserves required to grow in darkness sufficiently to penetrate the litter. It may also create an inappropriate germination bed where seedlings cannot reach the soil minerals, thus failing to become established. Litter also preferentially transmits longer wavelengths of light, reducing the R/FR ratio to a level that can be inhibitory for germination of photoblastic seeds (121, 123).

Litter disturbance is an important factor determining the germination of gap pioneers. In tropical forests, root and crown areas of felled trees offer different possibilities for the growth of plants from seed, due in part to contrasting degrees of litter disturbance (90). Alternatively, the presence of litter may be an important factor determining the inability of the seeds in a seed bank to colonize small gaps in some tropical forests (91, 128).

## CONCLUSIONS

As a consequence of the enormous diversity of plant taxa and life forms that characterize this plant community and the multiple phylogenetic origins of the plants, tropical rainforest seeds are also remarkably diverse in: size, shape, seasonality of production, volume of the seed crop, number of seeds per fruit, seed size, shape, morphology and anatomy, moisture content, nature of reserves, and presence of secondary compounds (35, 36, 50, 60, 79, 94).

Physiological characteristics of seeds such as basal metabolism at dispersal, the presence or absence of photosynthetic metabolism in the embryo, and the duration of dormancy and speed of germination on the ground also show great variability, although less information is available (116).

It seems that the plants that become established in the undisturbed forest floor have less complex environmentally regulated dormancy mechanisms than those established in scattered or occasional discontinuities of the forest environment like gaps (101, 119, 122, 126). Unfortunately the amount of information available on physiology of dormancy of rainforest seeds is too

limited to generalize on the prevailing dormancy mechanisms of the different ecological groups of plants.

A small number of papers deal with the detection of the comparative germination response of seeds of various species in natural conditions, over a varied range of environmental conditions (38, 92, 97, 95). In order to further understand the patterns of seed longevity and germination in the tropical rainforest, carefully controlled studies of seed behavior in the field are still required; most of the experimental research done in nurseries or laboratories lacks meticulous seed handling, simulation of the natural environmental conditions, or ecological orientation. Hence only shallow generalizations can be made about viability, dormancy, and germination patterns, based on a few relatively well-known examples, including a handful of species that have been the object of carefully controlled ecophysiological studies.

Basic information on seed behavior is still required in order to develop techniques for proper field collection, handling, conservation and storage of seeds, and for their use in the production of saplings in nurseries. Such techniques will allow the improvement of forest replanting and reforestation with native species in the humid tropics of the world (127).

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