GERMINATION OF SEEDS OF TROPICAL RAINFOREST SPECIES: RESPONSES TO TIME AND LIGHT QUALITY

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STATEMENT ON SOURCES

DECLARATION

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Abstract

There is scant information available about the seed ecology of species of the tropical rainforests of Australia. This is the first known investigation of a large number of species from the rainforests of north east Queensland in relation to time and to light quality. A total of 136 seed lots representing 130 species were randomly collected and germinated in four different light treatments – white, red and green light and darkness. For the sake of convenience, darkness is at times referred to as black light in this paper.

Time to germination was assessed in white light, and recorded over 12 or more weeks. Results were obtained for 112 seedlots. Sixty percent germinated within the first six weeks after sowing, 23 percent took 7-12 weeks, and the remaining species germinated after 12 weeks, the longest recorded period being 31 weeks. Species with rapid germination tended to have highly uniform germination and a high germination capacity. Over 60 percent of the species germinating in the first two weeks had highly uniform germination, and this fell to 28 per cent for species germinating in the following four weeks.

Germination in the three ecologically relevant light treatments (white, green and black light or darkness) is presented in a conceptual framework (a ternary plot) that allows for easier interpretation of the relative light responses of the test species. It is visually apparent that the largest group (57 per cent of the species which yielded results) is made up of species which show no germination response to light quality. Other recognisable groups are species for which germination is facilitated by, or occurs only in white light, and those demonstrating inhibition of germination in green light. Significantly, there are no species with maximum germination in green light, which simulates canopy shade. This indicates that while many species are capable of germinating in shade, germination levels are not maximised in this light environment for the tropical rainforest species in this study.

For all species there is a weak negative correlation between percentage of total germination in white light and seed size. Within related groups of species, smaller seed size is associated with a germination response to light quality. Early successional species, as expected, generally germinated better in white light, and distribution patterns of some species suggest that dispersal mechanisms could be important in transporting the seed to a suitable light environment for successful germination.

LIST OF TABLES

LIST OF FIGURES

Glossary

Avoidance and preference terms of convenience used at times to describe respectively inhibition and facilitation of germination in particular light environments

Biota the population of living organisms in general

Black light a term of convenience used to describe darkness or the absence or light

Cretaceous period the last period of the Mesozoic era, from about 140 to 70 million years ago

Diaspore the reproductive unit (seed or fruit) of a plant at dispersal

Differential dormancy (non-uniform dormancy), describes the situation when individual seeds in the same seed crop germinate at different times after sowing

Dormancy the state of a viable seed which fails to germinate even when suitable external conditions exist (adequate water, oxygen and a favourable temperature)

Embryonic axis a stem like axis with apical meristems at both ends

Endogenous dormancy dormancy associated with seed related factors

Germinability capability of germination

Germination capacity the proportion of a sample of seeds apparently capable of germinating

Germination the process by which the embryo within the seed develops into a new plant. The first visible sign of germination is often the emergence of the radicle from the seed coat

Gondwana southern land mass composed of South America, Africa, India, Australia and Antarctica, before continental drift moved these continents to their present positions

Herbivory consumption by a plant eating animal

Hypocotyl the portion of the embryonic axis between the cotyledons and the radicle

Imbibition the passive uptake of water, as in seeds before germination

Light quality the wavelength or spectral quality of light

Pericarp the fruit wall, which develops from the wall of the ovary, and thus is composed of maternal tissue

Pfr the far red light-absorbing form of phytochrome which is physiologically active. It absorbs light at 730 nm (far red light) and is converted to Pr, the physiologically inactive form of phytochrome.

Photoblastic describes a seed whose germination is influenced by light. Seeds that are stimulated to germinate by light are described as positively photoblastic; seeds whose germination is inhibited by light are said to be negatively photoblastic. The response to light is apparently mediated by phytochrome. In this paper, photoblastic is used to describe plants that are stimulated to germinate by light.

Phytochrome a light sensitive protein-based plant pigment present in small quantities in many plant organs, including seeds. It exists in two photoconvertible forms: Pr, the physiologically inactive form and Pfr, the physiologically active form. Phytochrome is involved in a variety of plant responses including seed germination.

Pr the red-absorbing form of phytochrome which is physiologically inactive. It absorbs light at 660 nm (red light) and is converted to Pfr, the physiologically active form of phytochrome.

Propagule see diaspore

Quiescent describes temporary suspension of development because of unfavourable environmental conditions

R:FR ratio the ratio in photon flux density (PFD) at 660 nm and 730 nm, the absorption peaks of the red and far red absorbing form of phytochrome (P) respectively.

Radicle the embryonic root

Seed the matured ovule, formed following fertilization

Testa the outer coat of the seed

Uniformity of germination a measure of the synchrony or simultaneity of germination of each species, reflected in the steepness of the germination curve over time.

Vermiculite a clay mineral formed from mica.

Viability capability of living

TABLE OF CONTENTS

CHAPTER ONE
GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 General Introduction

Tropical rainforests are well known to be the most complex and diverse of all terrestrial ecosystems. In Australia, they represent a continuity of a tropical lifeform that has existed since the Cretaceous period, when Australia was still part of Gondwana (Curtis 1990). These forests house the progenitors of Australia's flora and are a unique living record of botanical history. Although rainforest patches occur in the Kimberleys, the northern part of the Northern Territory and Cape York, Australia's tropical rainforests are best developed in the humid tropics of north east Queensland, where approximately 750,000 hectares lie in the area between Townsville and Cooktown. The unique values and characteristics of these forests have been recognized by their inclusion on UNESCO'S World Heritage List in 1988.

Elsewhere in the world, tropical rainforests occur in countries which are still developing economically and are experiencing strong population growth. In many of these areas natural rainforests are being exploited unsustainably for timber and other forest products, or being converted to agricultural land uses. In Africa and Asia traditional shifting cultivation is a major cause of forest clearing, whilst in Central and South America vast tracts are cleared for ranching (Lanly 1995). Although forests are always changing in response to natural stimuli, the obvious and rapid changes in our time as the result of human disturbances are unprecedented in their rapidity, intensity and extent (Hopkins 1990).

The perilous state of the world's tropical rainforests has been noted by many authors (Shugart *et al.* 1980, Whitmore 1984, Vazquez-Yanes and Arechiga 1996, Terborgh 1999). Gomez-Pompa and Vazquez-Yanes (1974) reported that primary rainforest vegetation was rapidly being replaced by secondary vegetation, with native biota either disappearing or adapting to the situation, especially in tropical lowland areas. The situation has not changed since this was written over 25 years ago. Shugart *et al.* correctly predicted in 1980 that the conflict over rainforest conservation versus rainforest utilisation would escalate with growing awareness of the importance of rainforests as global reservoirs of carbon.

The ramifications of forest clearing and the subsequent loss of biodiversity are well expressed by Gomez-Pompa and Bainbridge (1995).

> "Many important species and biotypes and the communities in which they are found, have been lost or are threatened. These losses are more than a simple biological tragedy because these forests play an important role in regional and planetary metabolism. They also contain many species of economic importance and thousands of as yet unstudied species with potentially important economic value. They are the major source of genes for future uses in genetic engineering."

The destruction of rainforests is not just a biological problem. Social and economic problems are both a cause and a consequence of exploitation of these forests (Eaton 1996), and long term solutions have yet to be found.

There is increasing interest worldwide in practical ways to halt the current rates of loss of tropical rainforests and to restore and rehabilitate forest in already degraded areas. Although part of the solution will be based on economic and social programmes (*e.g.* improved education of local communities), there are still major impediments related to our level of understanding of key biophysical processes in tropical forests.

One important area of rainforest ecology with significant practical applications in which we have surprisingly little knowledge is the ecology of seeds and seedlings. Seeds are the primary regenerative propagules of most rainforest plant species and a better understanding of their ecology will aid in predicting the ability of forests to recover naturally from disturbance as well as being relevant to reforestation and rehabilitation programmes. Grubb (1977, p108) suggested that the way in which regeneration (or replacement) occurs in plant communities is "of great importance not only for understanding species-richness as such but also for understanding the basic processes of evolutionary divergence in plants and for the management of plant communities in conservation".

The purpose of this study is to examine aspects of the germination of rainforest plants. In particular, the effects of light quality on germination, time to germination and other seed attributes will be examined. The results pertain to a suite of species of the tropical rainforests of far north Queensland, and have relevance for the practice of regeneration and rehabilitation as well as contributing to an understanding of the mechanisms generating and maintaining diversity of tropical species (the "regeneration niche" concept proposed by Grubb (1977)).

1.2 Literature Review: Effects of Light Quality on Seed Germination in Rainforest Plants

Introduction

Although vegetative reproduction occurs, especially in areas exposed to high levels of natural disturbance, most plants of the tropical rainforest regenerate under natural conditions from the germination of seeds. An understanding of the factors involved in this process will enable us to promote regeneration both in the field and the nursery by manipulating or providing appropriate conditions for successful germination.

Germination is the process by which the embryo develops into a new plant. It starts with imbibition by the quiescent, dry seed and ends, strictly speaking, with the elongation of the embryonic axis (Bewley 1997). In an experimental situation, completion of the process is accepted to be visible germination, when the radicle penetrates the tissue surrounding the embryo (Itoh 1995, Garwood 1996, Bewley 1997, Demel and Granstrom 1997). The failure of a seed to germinate in apparently suitable conditions of light, temperature, air and moisture is termed dormancy.

In general, seeds of the tropical rainforest are reputed to have the shortest dormancy of any ecosystem (Longman and Jenik 1987), with predominantly fleshy seeds that are obligate rapid germinators. There are, however, many rainforest seeds with dormancy, often associated with specific light or temperature requirements. Species with dormancy are more frequently found in seasonal tropical rainforests (Vazquez-Yanes and Orozco-Segovia 1984).

The majority of the seeds of mature forest species are light insensitive and soft coated, and tend to germinate rapidly. Some, however, take an extended time to germinate, and these are considered to display some form of dormancy. Baskin and Baskin (1998) suggested germination that occurs after four weeks indicates the presence of endogenous dormancy. For non-pioneer species, dormancy is seen in seasonal forest species where lack of water during the dry season prevents germination. Other species have hard seed coats, which are suggested to be associated with the presence of immature embryos or an inhibitory substance in seeds (Vazquez-Yanes and Orozco-Segovia 1990). Moisture content of seeds at dispersal also affects timing of germination. Seeds with higher moisture contents germinate before less moist seeds, with the timing of germination probably regulated by the balance between water gain from the soil and evaporation to the surrounding atmosphere (Foster 1986).

Factors affecting the germination of tropical rainforest plants

Germination is influenced by the interactions between environmental factors and genetically acquired characteristics of the seed. The relevant environmental factors affecting germination include light, temperature, moisture and aeration (Baskin and Baskin 1998). The specific requirements for these vary with the morphology and physiology of the seeds. Additional factors are herbivory, attack by pathogens and seed dispersal. Both herbivory and attack by pathogens can affect the viability and germinability of seeds and the extent of this effect can be reduced by dispersal of seeds to a site removed from the parent tree, from sibling competition and from breeding sites for herbivores and pathogens (Vasquez Yanes and Orozco Segovia 1990).

Seed size

Seed related factors affecting germination include seed size and morphology and the maternal light environment encountered by the seed during development.
Seed size is believed to be a compromise between benefits and costs. For a given investment in reproduction, the benefit of large seeds and more competitive seedlings is traded off against the biological costs of large seeds, which include a greater risk of

predation, a reduction in dispersal distance and a lower chance of survival in the soil seed bank (Crawley 1997). Conversely, small seed size is associated with the production of greater numbers of seeds with an improved chance of some escaping predation, and the possibility of dispersal to a greater distance from the parent tree.

Seed size can affect both germination and survival. Wulff (1995) noted that within species, larger seeds are frequently produced in more shaded habitats, where they offer the possible advantages of being able to emerge from greater depths if covered by soil, litter or other vegetative cover. Green (1999) however, found that for the large seeds of *Chrysophyllum* sp. nov, seed size, although it varied more than 30-fold, had no bearing on germination from beneath litter. Large size may impart a greater tolerance of nutrient deprivation, and a competitive advantage in timing of germination.

Smaller seeds, by comparison, are advantaged by greater ease of dispersal and the capability rapid germination under suitable conditions, thereby escaping predation (Vazquez-Yanes and Orozco-Segovia 1990). These seeds often also form a persistent seed bank as a result of environmentally induced dormancy. Whilst smaller seeds are reported to often have lower overall germination than large seeds, in some conditions, germination of small seeds is higher possibly because of their greater surface to volume ratio and consequently greater access to water (Foster 1986, Wulff 1995).

Wulff (1984, 1995) found that for *Hyptis suaveolens,* seed size and germination response to light were strongly associated. Larger seeds had higher levels of dark germination, and also required lower levels of R:FR light for complete germination. Additionally, germination responses to temperature were different for large and small seeds of this species. This variation in seed size is advantageous in that the different sizes are favoured in different microsites. Insofar as larger size might be associated with a thicker seed coat, seed size could also be related to dormancy. The fact that there are differences in germination requirements among populations from different provenances raises the possibility that dormancy could be environmentally induced.

By clipping the leaves of seedlings, Armstrong and Westoby (1993) showed that larger seeds are generally better able to cope with loss of photosynthetic tissue or

carbon deficit. Thus large seeds should be favoured in situations such as deep shade where seedlings are likely to experience limited photosynthesis. Dalling and Harms (1999) demonstrated that for the tropical tree *Gustavia superba,* survival of pre- and early post-germination predation and damage was related to cotyledonary seed size. (See also Harms and Dalling 1997, Dalling *et al.* 1997.)

Grubb and Metcalfe (1996) claimed that seed size was adaptive in situations and for reasons other than survival in the shade. The authors compared light demanding and shade tolerant genera within the same subfamily or family and found that in 13 of 14 cases, shade tolerant genera had seeds of greater mass. Comparisons of species within the same genera showed that for eight of nine cases, the shade tolerant species had seeds of approximately the same or slightly lesser mass. They interpreted these results as supporting the theory that seed size has a low position in the hierarchy of attributes enabling establishment in the shade compared with physiological features determining carbon balance (see Grubb and Metcalfe 1996).

In contrast to the above findings, Davies and Ashton (1999) reported that for 11 sympatric species of *Macaranga* in Borneo, seed size was one of a number of attributes that covaried with the degree of shade tolerance. In Southern India, Murali (1997) found a strong correlation between seed size and days to germination, with smaller seeds germinating faster than large ones. It is also reported that species that fruit in the rainy season produced heavier fruits than those produced in the dry season. Lighter seeds in the drier months probably have less chance of surviving desiccation, but the fact that they can be produced in greater numbers may increase the chance of some seeds surviving.

These diverse findings suggest that there is no single clear answer to the question of how seed size relates to germination. Seed size has also been associated with seed dispersal. For tropical rainforests, the two principal modes of dispersal are by wind or by animals. There is evidence that the latter is more effective (Whitmore 1984). Large animal dispersed seeds, usually shade tolerant, establish mostly beneath the canopy because they are unlikely to reach a gap. Smaller seeds that are dispersed by wind or small animals and are frequently light demanding at germination, are more likely to

reach a sunlit environment and therefore to become an adult if they land in a gap than if they land in canopy shade (Schupp *et al.* 1989).

Both Hladik and Miquel (1990) and Forget *et al.* (1998) presented the idea of seed size being related to seed fate via the animal dispersers. Grubb (1998) proposed that seed size may be determined to a greater degree by dispersers than by perceived advantages at the establishment stage. He interpreted the smallest seeds (<1 mg.) as having the advantage of not being crushed by the teeth of dispersers, and the largest seeds (>2000 mg.) in terms of attracting large animal dispersers such as large mammals and cassowaries.

In addition to dispersal in space, dispersal in time is also an important aspect of the regenerative strategy of many species. Dispersal in time occurs when differential dormancy results in germination being staggered over time. Differential dormancy describes the situation where seeds produced at the same time take varying times to initiate germination. The relevance of this feature for species survival is obvious (Gutterman 1992).

Light

It has been recognised since the nineteenth century that light influences germination and that particular colours (wavelengths) of light promote germination whilst others inhibit it. Toole (1973) and Shinomura (1997) are just two of many authors who have outlined the observations and discoveries over time concerning the role of light in germination. A summary of these reports is given below.

In 1860, Caspary found that seeds of *Bulliadrea aquatica* showed higher germination in full sunlight than in diffuse light. A reverse reaction, the inhibition of germination of some seeds by light was demonstrated by Heinricher in 1903. Over time, data on both promotion and inhibition of germination by light accumulated, and further experimentation showed that light interacted with other factors - especially temperature - and also the maturity of the seed at harvest, the nature of the seed coat and other growth conditions.

In the mid 1930s, Flint and McAllister showed that light quality, or wavelength, was a significant determinant of germination: short exposures of less than one hour duration of wavelengths around 660 nm tended to promote germination and wavelengths around 730 nm tended to have an inhibitory effect. This led to the discovery in 1952 by Borthwick *et al.* of the photoreversible effects of red light (R) and far red light (FR) in promoting and inhibiting germination. The existence of a light-absorbing pigment in the embryo was deduced from germination responses to light treatments, and finally in 1959, the pigment phytochrome was isolated and identified.

The light environment of tropical rainforests

Light is considered one of the most important environmental factors affecting the germination and early establishment of seedlings of tropical rainforest plants. Changes in light quality following canopy removal, or fluctuations in soil temperatures following exposure for part of the day to direct sunlight, trigger germination in tropical pioneer species (Webb, Tracey and Williams 1972). Other triggers have been reported for temperate species (flush of nitrates, fluctuating soil moisture content or a wavelength independent increase in radiation known as the High Irradiance Response or HIR), but these have not been shown to operate in tropical rainforest ecosystems (Swaine and Whitmore 1988). In reality, it seems that germination is affected by the simultaneous action of a number of environmental factors in the field, from the period of seed maturation until the time of germination (Frankland 1981, Pons 1992).

Numerous studies have noted the variation in the light environment of tropical rainforests. Even within a single habitat, the light climate can change dramatically over the course of a day (Chazdon and Fetcher 1984). Investigation of the light environments of old growth, secondary growth and selectively logged stands of moist tropical forest in Costa Rica showed that while mean light availability did not differ between stand types, the variance and frequency of light availability did, resulting in dynamic light conditions of the forest understorey which could be described as a 'moving window' of light availability (Nicotra *et al.* 1999). Tropical rainforests contain some of the brightest and darkest of terrestrial habitats (Mulkey *et al.* 1996). This variation in one of the most important environmental features of the tropical

rainforests would be expected to affect plant characteristics, both morphologically and physiologically (Mulkey *et al.* 1996).

The light environment is described by its fluence or energy, duration and quality. It is this latter property of light quality as it affects germination that is investigated in this study. Light quality refers to the spectral composition or wavelength of light. The light climate to which seeds are exposed is usually described in terms of the ratio of red light to far red light (R:FR ratio). This is the ratio in photon flux density (PFD) at 660 nm and 730 nm, the absorption peaks of the red and far red absorbing form of phytochrome (P) respectively. The R:FR ratio of daylight is approximately 1.2, whilst under a forest canopy this is reduced to approximately 0.2 (Pons 1992).

Historically, most of the analytical and descriptive literature relates to temperate species and forest systems (Black 1972, McCullough and Shropshire 1970, Frankland 1981, Bartley and Frankland 1982, Pons 1992, Bewley and Black 1994, Bewley 1997). Over the past few decades, there has been an upsurge in tropical vegetation studies. In the 1980s "gap-phase replacement" research to uncover the processes of establishment and growth was a prominent area of ecological activity (*e.g.* Brokaw and Scheiner 1989, Hartshorn 1989) even though 1% or less of tropical rainforests are recent gaps (Connell 1989, Schupp *et al.* 1989).

Pioneer species and climax species

An important and enduring contribution to this area of study came from Swaine and Whitmore (1988) who proposed that rainforest tree species should be divided into two guilds or groups on the basis of their germination and establishment behaviour in relation to light. They defined these two groups as pioneer species and non-pioneer or climax species. They acknowledged that within these groups there is continuous variation, but argued that this proposed dichotomous classification would eliminate much of the confusion caused by imprecise definitions and subdivisions.

Pioneer species are defined as those whose seeds can only germinate in gaps in the forest canopy open to the sky, and in which full sunlight reaches ground level for at least a portion of the day (Swaine and Whitmore 1988). Obviously, pioneer species

can also regenerate in open areas or on forest margins. These species reputedly also require full sunlight for seedling establishment and growth. Dormancy caused by hard seed coats or unsuitable environmental conditions, especially light, is a feature associated with pioneer species. Typically, pioneers produce large numbers of small wind or animal dispersed seeds from an early age, and have rapid growth in the high light conditions in which they flourish (Kitajima 1996). More recently, pioneers have been described as those that germinate establish and grow to maturity only in treefall gaps (Garwood 1996), and as those species that germinate and establish in recently disturbed sites, and complete their life cycle without being overtopped by neighbouring trees (Ackerly 1996). Although these features are a useful starting point to defining pioneer species, there are many species often regarded as pioneers that do not adhere strictly to these descriptions.

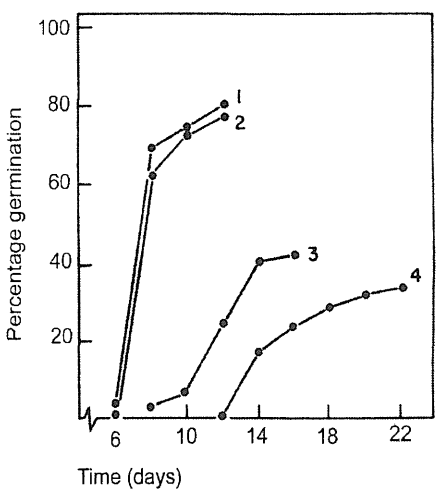


Figure 1.1 Time-course of germination of *Piper auritum* under simulated canopy spectra with varying R:FR ratios. 1-R:FR=2.3; 2-R:FR = 0.58; 3-R:FR = 0.23; 4-R:FR = 0.20 (from Vazquez-Yanes and Smith 1982)

Figure 1.1 illustrates the effect of reduced R:FR ratio on germination of *Piper auritum* under simulated canopy light conditions. *Piper auritum* is a typical pioneer tree in the lowland tropical rainforests of south-east Mexico, central America and northern South America. Under experimental conditions as the R:FR ratio declines, simulating increased shading, germination is both delayed and reduced. Under natural forest conditions, this species does not germinate under canopy shade The authors speculate that the difference between natural and experimental conditions might be due to a

lower R:FR value inside the forest, or a higher fluence rate in the experimental situation (Vazquez-Yanes and Smith 1982).

Climax species are those whose seeds can germinate in the shade of the forest, and whose seedlings can establish and survive in forest shade. They may also germinate in sunlight, and seedlings of many climax species (*e.g. Cardwellia sublimis, Litsea leefeana*) may not survive in shade for long (Swaine and Whitmore, 1988). Given the broadness of this definition, it might be more appropriate to use the term 'non-pioneers'.

Climax species typically produce fewer, larger seeds than pioneer species, with greater reserves reputedly for germination and establishment in low light environments. Further subdivisions of this group are frequently made based upon successional status, or the timing of recruitment into the forest community (Kitajima 1996).

The vast majority of rainforest tree species are climax species (Brown and Jennings 1998), although human disturbance of the forests has resulted in an increase in the number of pioneer species in many areas. Since climax species cover a broad spectrum of light environments from the extremely deep shade of the forest interior to conditions barely removed from high light, it is to be expected that regenerative characteristics will be diverse.

The pioneer/climax classification proposal was regarded by some as too simplistic. Martinez-Ramos *et al.* (1989) argued that this framework restricted species to just one pathway to maturity, defined by light requirements early in life. In reality, there are numerous other biotic and abiotic factors which come into play during the life of forest plants including diaspore dispersal, competition with other plant lifeforms, the effects of litter depth and soil disturbance, herbivory, pathogens, and the effects of drought or nutrient limitation (Nicotra *et al.* 1999). Brown and Jennings (1998) also questioned the paradigm, expressing their belief that the forest light climate, on its own, does not provide an appropriate environmental gradient for niche differentiation of a large number of climax species.

The purpose of this simplified classification was to facilitate recognition of patterns and formulation of predictions of forest behaviour. The persistent use of these terms and the divisions they signify suggest that they do have some relevance in studies of rainforest ecology. At the very least, this division of species based on mode of regeneration in light provides a framework within which all species can be assessed.

Other authors have also contributed to the literature on factors affecting seed germination in tropical rainforest plants. Vazquez-Yanes and Orozco-Segovia (1982, 1984, 1990, 1993) reported extensively on the ecophysiology of germination and dormancy as influenced by light quality and other factors. They found that the seeds of almost all the pioneer species studied exhibited a requirement for light for germination (Vasquez-Yanes and Orozco-Segovia 1990). For *Piper auritum* it was reported that the phytochrome balance in the seeds was affected by the maternal light environment during ripening of the infructescence. The authors suggest this may have created intraspecific variation in responses of seeds to different light environments.

Garwood (1983) conducted a community study of germination in the seasonal tropical forest on Barro Colorado Island, Panama and identified the effect of seasonality on germination and dormancy of over 150 species. In a later study Garwood (1996) explored the relevance of seedling morphology in regeneration. Augspurger (1984) studied the light requirements of neotropical tree seedlings in Central and South America while Hladik and Miquel (1990) investigated seedling type and germination ecology in the tropical rainforests of Gabon. Probably the best known descriptive studies were those conducted over a number of years by Ng in Malaysia (1975 to 1992).

Australian tropical rainforests have been similarly scrutinised but there has not been a published study of germination of a large number of species. Hopkins (1990) and Hopkins and Graham (1984, 1987) investigated many aspects of disturbance and change. Metcalfe (1996), Grubb (1998) and others pursued establishment, seed size and shade tolerance amongst other topics, and Connell continues to study recruitment over an extended time period in an undisturbed plot on the Atherton Tablelands.

Metcalfe's 1996 study of germination responses of 11 small seeded tropical rain forest species exposed to different spectral compositions in Singapore identified four germination strategies. Seeds of shade tolerant species were exposed to three light environments – daylight, green shade and darkness, with the aim of determining if they could germinate in shade or required a gap to germinate, becoming shaded at a later stage. Results indicated that the 11 species could be placed into four groups according to germination response to light environment. *Melastoma* germinated only in the daylight treatment. Germination of three *Ficus* species was reduced in percentage and delayed in time in darkness, and even further in green light. *Pternandra* and *Urophyllum* species took progressively longer to germinate in green shade and darkness, and germination percentage was greatly reduced in darkness. The final group, represented by *Gynotroches* and *Pellacalyx* germinated equally in all light treatments, but after a longer time in darkness and green shade. The light treatments in this study were variations of the R:FR ratio in the light environment to which seeds respond *via* the photoreceptor phytochrome.

Control of germination by phytochrome

It has been demonstrated that the photoreceptor phytochrome is the means by which plants monitor the light environment, and that it is the ratio of red to far red light that either promotes or inhibits germination (Shinomura 1997, Casal 2000). In addition to phytochrome, there are other photoreceptors that perceive the light environment, including cryptochromes, phototropin and an unidentified UVB receptor (Shinomura 1997).

In a study of the effects of light quality on seed germination it is necessary to first understand the role of phytochrome. Phytochrome (the word is used in the singular and the plural, even though more than one phytochrome is known to exist) is the name of a group of dimeric chromopeptides which exist in two photoconvertible forms – **Pr**, the red light absorbing form, and **Pfr**, the far red absorbing form. Pr is considered to be the physiologically inactive form, and Pfr the physiologically active form. Synthesis of phytochrome in the plant is in the Pr form, and this is transformed by red light absorption to the active Pfr form. Pfr reverts to the inactive Pr form by absorption of far red light. The absorption maxima of Pr and Pfr are approximately

660 and 730 nm respectively, but because there is an appreciable overlap between the two forms, light absorption produces a mixture of Pr and Pfr. Conversion between Pr and Pfr involves a series of short lived intermediates. Phytochrome in seeds can revert in darkness from Pfr to Pr, a process that could be important in reducing Pfr in seeds buried under soil (Casal 2000).

In addition to germination, other aspects of plant growth and development including seedling de-etiolation, vegetative growth, organ orientation and the progression to reproductive development are also light affected (Casal 2000). It seems that the light sensitive region of seeds is the hypocotyl-radicle region of the embryo (Salisbury and Ross 1992). Photo transformation of Pr to Pfr occurs only in moist seeds in response to the R:FR ratio of light to which the seed is exposed. At dispersal the balance between Pr and Pfr will depend largely on the optical properties of the tissues covering the seed, and on whether or not the fruit developed in the open sunlight, or in the shade of green leaves (Casal and Sanchez 1998).

In seeds that dry out at maturity, the Pr/Pfr balance will be arrested as it was immediately prior to the seed drying. For many rainforest species, there is no drying out stage, so the balance between the active and inactive forms of phytochrome could theoretically change right up to the point of germination. Since high moisture content is generally associated with climax species and these tend not to be light sensitive, the effects of light and phytochrome are not as well defined as for light sensitive species. Germination in darkness, a capability attributed to climax species, does not mean that such species have no phytochrome in their seeds, but rather that their seeds already contain sufficient Pfr for germination induction (Toole 1973, Taylorson 1982), or that Pfr is not needed for germination. It is not yet possible to determine which of these mechanisms is in operation in any particular situation.

Cresswell and Grime (1981) demonstrated a negative relationship between germination in darkness and the chlorophyll content of tissues surrounding the embryo. Green tissue around the seed has the same effect as leaf canopy shade. Both situations result in a high level of Pr in the seed, associated with low levels of germination in darkness.

Much of the exploratory work on phytochrome has been conducted on temperate species with small, rapidly germinating seed, such as *Lactuca sativa* and *Arabidopsis thalliana.* Five phytochromes have been identified in *Arabidopsis thalliana* – Phytochrome A (phyA) to phytochrome E (phyE) (Casal 2000). The availability of mutant varieties lacking various photoreceptors has enabled the identification of specific pigments involved in interaction between photoreceptors, light and plant responses (Shinomura 1997; Casal 2000).

PhyA and phyB are perhaps better understood in relation to germination than the other photoreceptors. PhyA appears in seeds after imbibition has proceeded for several hours. PhyB exists in dry seeds, and plays a role in the germination of dark imbibed seeds (Casal and Sanchez 1998). Other phytochromes could also play a part. The action of the different types of phytochromes in responding to light of varying wavelengths is also fluence dependent.

Three types of germination responses to light quality are recognised in light sensitive species (Aamlid and Arnsten 1998), and are described in terms of fluence.

1 the very low fluence response (VLFR) mediated by phyA
2 the low fluence response (LFR) associated with phyB and other phytochromes (but not phyA)
3 the high irradiance response (HIR). The phytochrome involved in this response has not been identified, but may be phyA. The HIR occurs only under far red light, with maximum inhibition of germination at 710-720nm. This correlates well with phytochrome cycling between Pr and Pfr (Casal and Sanchez 1998).

The VLFR is induced irreversibility by irradiance with low fluence light in a wide range of wavelengths. The LFR is photoreversible and responds to red and far red light at fluences higher than the VLFR by four orders of magnitude. In seed germination, the HIR operates to inhibit germination under prolonged irradiation with far red light, but an opposite reaction under red light does not occur. The HIR inhibits germination in systems where the VLFR and the LFR promote germination (Casal and Sanchez 1998).

The physiological changes caused by phytochrome in inducing germination have been studied primarily in seeds with dormancy imposed by the tissue surrounding the embryo. Phytochrome has been shown to act on the capacity of the embryo to grow and on the softening of the endosperm (Casal and Sanchez 1998).

Studies of the various phytochromes and the responses they induce in plants are constantly providing new information. At present, it appears that all three modes of phytochrome action, as described above, are possibly involved in field responses. The VLFR is believed to be associated with germination resulting from soil disturbance caused, for example, by animals such as chowchillas, feral pigs and brush turkeys turning the soil. The LFR is demonstrated in germination induced by light with a high R:FR ratio as occurs in gaps. The action of the HIR appears to be in preventing the germination under canopy shade of seeds which require a high R:FR for germination (Casal and Sanchez 1998).

The more recent literature is generally consistent in descriptions of these three types of light responses. Most confusion is seen in references to the HIR. In earlier reports (prior to around 1990), the term HIR was used to describe responses to continuous light of any wavelength, and without testing to see if short pulses of light could produce the same result (Casal and Sanchez 1998). This term is correctly used to describe a light response when equal fluences do not give the same result under continuous or pulsed light *ie* there is reciprocity failure (Casal and Sanchez 1998). In practical terms, for tropical rainforest species, continuous light with a high R:FR ratio would most likely prevent germination because of the death of the seed as a result of desiccation, rather than because of any phytochrome response.

The literature on germination responses to light for tropical rainforest species does not generally speculate on what type of reaction is involved, describing the light environment simply in terms of a high or low R:FR ratio, or sun, canopy shade or darkness. Augspurger (1984) described germination and survival of 18 species of wind-dispersed trees in terms of responses in sun and shade. Even when interpretations do include details of photoconversions, as in Vazquez-Yanes and Smith (1982), there is no mention of VLFR, LFR or HIR. To attempt to identify such reactions would be extremely difficult, because of the complexity of conditions

encountered by seeds in the field. In earlier years, the existence of phytochrome was deduced from plant/light reactions long before the substance was isolated and described. It seems that although we can identify the nature of reactions in the laboratory, we are still largely confined to deduction and inference in interpreting ecological responses in the field.

Conclusion

Despite the extent of recent ecological investigations, to date there has been no published information describing and detailing the germination behaviour of a large number of species of the Australian tropical rainforests. The aim of this study is to address some of the knowledge gaps in this area. The approach used was to collect as wide a range of species as possible with different seed characteristics and to seek answers to three particular questions:

a) What germination responses are displayed over time, by samples of seeds of a range of selected rainforest species of different lifeforms, collected from a range of habitats within the Wet Tropics Rainforest Region of far north Queensland?

b) What are the effects of four light quality treatments on the germination of a range of selected rainforest species of different lifeforms, collected from a range of habitats with the Wet Tropics Rainforest Region of far north Queensland?

c) Are germination characteristics and responses to light quality related to seed size, diaspore type, mode of dispersal and the maternal light environment?

To date, few studies have experimentally investigated or compared the responses of a range of species to different light qualities. For example, although pioneer species seem to be generally more dependent on light quality than climax species (*sensu* Swaine and Whitmore 1988), only two species appear to have been examined experimentally to determine the nature of the response and the underlying causal mechanisms (*Cecropia obtusifolia* and *Piper auritum*: Vazquez-Yanes and Smith, 1982).

It is also interesting that despite the importance of light as a factor regulating seed germination, there appears to be no conceptual framework or model within which responses to light quality have been evaluated. Such a conceptual model could be based on either requirements for or facilitation of germination in a particular light quality ('preference') and/or on inhibition by particular light quality conditions ('avoidance'). In addition to exploring the three questions posed above, a conceptual model is proposed to present germination responses to light quality. Since this project was conducted over only one growing season, the results presented are not regarded as definitive of germination responses to light quality. The emphasis is rather on developing a model to demonstrate the different responses to the light spectrum for a suite of species in the time frame of the study. The model can then be used for comparative purposes over time and with other species.

In the next two chapters, the germination behaviour of seeds of more than 100 species of Queensland rainforest plants is examined. In Chapter Two, the time to commencement of germination, and aspects of uniformity and capacity of germination in white light are investigated. In Chapter Three, germination of these species is compared in four light quality treatments (white, red, green and 'black light' or darkness) and the species are categorised into light response groups on the bases of a statistically significant response to light treatment, and a simple conceptual model of germination facilitation or inhibition for each light quality. In Chapter Four, relationships between germination characteristics of these species and other attributes are explored.

CHAPTER TWO
GERMINATION AND TIME

2.1 Introduction

Seeds are the primary regenerative propagules of most tropical rainforest plants. An understanding of seed ecology, and in particular their germination characteristics and requirements, is fundamental to interpreting patterns of seedling recruitment in forests. It also has important applications both in production of nursery stock for timber plantations and for forest rehabilitation schemes and in the future development of direct seeding techniques for broad-scale rehabilitation of degraded former rainforest landscapes.

Selected germination characteristics of seeds of tropical rainforest species have been investigated in a number of previous studies (e.g. Ng 1980, Garwood 1996). Not surprisingly, a range of germination 'behaviours' has been documented, including significant differences between species in the time taken for germination to occur (Ng 1973 and 1980, Garwood 1983).

Most tropical rainforest species examined to date have been reported to germinate within the first 6 weeks following dispersal (Hopkins and Graham 1987, Garwood 1989, Whitmore 1990, Vazques-Yanes and Orozco-Segovia 1993, Demel and Granstrom 1997), with viviparity (where germination takes place whilst the diaspore is still on the parent tree, commonly encountered in mangroves) even occurring in some taxa (e.g. *Pithecelobium racemosus*: see Vazquez-Yanes 1984). The ecological advantages to rainforest plants of this generally rapid germination are postulated to include avoidance of the hazards posed by desiccation, burial, predation, disease and competition (Ng 1978, Fenner 1985, Foster 1986). The dominance of rapid germination as a strategy in tropical rainforests is reflected in these communities having the shortest 'ecological longevity' of seeds (the average time between seed maturation and germination) found anywhere (Foster 1986, Longman and Jenik 1987).

Despite the dominance of rapid germination, delayed germination associated with seed dormancy is also well documented in a range of tropical rainforest species. Dormancy is an especially common characteristic of seeds of some pioneer and high-light demanding species that occur in the soil seed banks and of species from markedly seasonal rainforest environments (e.g. Garwood 1983, Vazquez-Yanes and Orozco-Segovia 1984, Hopkins and Graham 1987). Different species vary considerably in the periods for which they can remain dormant; reports range from several weeks to many years. Seed burial experiments have shown longevity amongst many species in the soil seed bank is achieved *via* an enforced dormancy mechanism (commonly a specific light or temperature requirement) or by the presence of hard, often woody, seed coats (Hopkins and Graham 1987).

The germination requirements of most species from Queensland's tropical rainforests are poorly understood. Although there have been detailed investigations of composition and attributes of seeds that comprise the soil seed banks in lowland forests (Hopkins and Graham 1987), there have been no other published studies of the germination characteristics of a wider range of species. This chapter reports the results of a survey, conducted under shadehouse conditions, of the time taken for germination to commence in white light in more than 100 species from north Queensland rainforests. Uniformity (synchronicity) and capacity (proportion of potential maximum) of germination are also examined.

The times recorded for initiation of germination in this study may differ for some species from those recorded elsewhere (A.K. Irvine personal communication). Variation between species and provenances can explain part of this, and it is also probable that the age of seeds collected is relevant. For seeds which do not dry out at maturity, development is continuous from dispersal through to germination, so that fallen seeds might be expected to germinate in a shorter time than seeds taken from trees.

2.2 *Materials and Methods*

Collection strategy

Mature fruits and seeds of rainforest plants were collected opportunistically during 1997 and 1998 from both upland and lowland rainforest areas within a 150 km range of Cairns, North Queensland (16°55'S, 145°50'E). Maturity was determined by comparing a range of seeds from each species, using knowledge acquired during earlier field studies. The objective was to collect as large a number of species as logistically possible that represented different life forms, ecological behaviours, fruit and seed types and sizes. It was not intended, and not possible, to stratify the study and collect equal numbers of representatives of each of these groups (because of a lack of basic information on the timing and reliability of fruiting, and the short apparent 'availability' of fruit and seed crops of some species). As a consequence, the collection strategy was largely opportunistic, relying on frequent visits to a range of forest areas and collection of whatever fruits and seeds were available in adequate quantities for the research. Four species known from a pilot study to have very delayed or erratic germination (*Beilschmiedia bancrofti, Elaeocarpus angustifolius, Endiandra palmerstonii, Alphitonia petrei*) were encountered fruiting during collection visits but were deliberately excluded from this study because of the time limits imposed on observations.

When available, some species were collected more than once. This was to investigate within species variation and to act as 'back-up' collections in case of infestation by insects and pathogens.

Seed collection and processing

Each individual collection comprised at least 170 seeds of each species. Wherever possible, fruits and seeds were collected from more than one tree, but always from the same provenance. Only apparently sound, clean fruits and seeds were collected.

Care was taken to ensure that seeds were not exposed to light from the time of collection until they were sown into germination trays in the shadehouse. In the field,

diaspores were collected into paper bags that were then placed inside black plastic bags. Unopened dehiscent fruits were collected from trees on which some fruits had already opened, and allowed to open in a cool dark environment. Sound freshly fallen fruit was also collected from beneath some parent trees.

Fruit was returned to the laboratory and stored in a cool dark room (temperature range 10°C to 22°C) until it was processed under a green 'safe' light, as soon as possible after collection, but usually within 1 to 7 days.

Processing of most fruit involved extracting seeds from fleshy pericarps and woody capsules, removing arils (where present) and soaking in water for 1 to 3 hours to remove insect predators. Processed seeds were then immediately sown onto trays in the shadehouse.

Germination conditions

Four replicates of 10 seeds of each species were placed on vermiculite in seed trays. Very small seeds were placed on pre-boiled muslin to facilitate observation. Seed trays were placed on tables in two shadehouses (Sarlon 70%), with two replicates of each seedlot in each shadehouse. Clear polyester filter material with no selective filtering properties (Roscoe Filter supplied by Bytecraft) and neutral shadecloth (Sarlon, 70%) mounted on metal frames formed a canopy over each table. Automatic sprinklers operated for 5 minutes six times per day to keep the vermiculite moist. Temperatures within these white light canopies ranged from extremes of 7°C to 39°C during the course of the survey, however, average daily temperatures for most of the period were between 16°C and 26°C.

Germination assessments and data analysis

The number of individuals that had germinated (defined as the visible emergence of a radicle from the seed coat) in each individual replicate was recorded weekly where possible during the first 12 weeks after sowing. Seedlots that had not germinated after 12 weeks were removed and transferred to another shadehouse in which the

temperature and moisture conditions were less well regulated. These seedlots were assessed occasionally for occurrence of germination for up to 12 months.

The speed at which different species germinated was examined on the basis of mean germination percentage from the four replicates over time. Species were classified as early, intermediate, or late germinators based on the classification used by Garwood (1996) that is outlined below:

Germination class	*Time to commencement of germination*
early	six weeks or less
intermediate	seven to twelve weeks
late	over 12 weeks

In addition to speed of germination, both (i) uniformity of germination and (ii) germination 'capacity' were assessed using criteria defined by Bewley and Black (1994).

Uniformity of germination, a measure of the synchrony or simultaneity of germination of each species, is reflected in the steepness of the germination curve over time. Only species that germinated during the first 9 weeks after sowing were included in this assessment because it was impossible to gauge the final level of germination for later germinators.

Germination capacity, the proportion of seeds apparently capable of germinating under the conditions of this study, was also assessed. Since germination was only recorded regularly over a limited time period of 12 weeks, the assessment of germination capacity is only valid for those species that reached a plateau or maximum level within that period.

2.3 Results

Species collected

One hundred and thirty six collections comprising a total of 130 species were made over the course of the study. These are shown in Table 2.1. The species collected represented a range of lifeforms (trees, shrubs, vines, herbs, palms and sedges), and included five introduced species that are common weeds on the fringes of rainforest (*Ardisia, Lantana, Ligustrum, Rivina* and *Solanum* spp.). Figure 2.1 shows the collection sites.

Despite care taken to use only sound seed, 23 seedlots either rotted in the shadehouse, or failed to germinate in white light. One species, *Glochidion philippicum,* was accidentally exposed to light, and so was excluded.

Table 2.1 List of species arranged by Family, showing place and date of collection

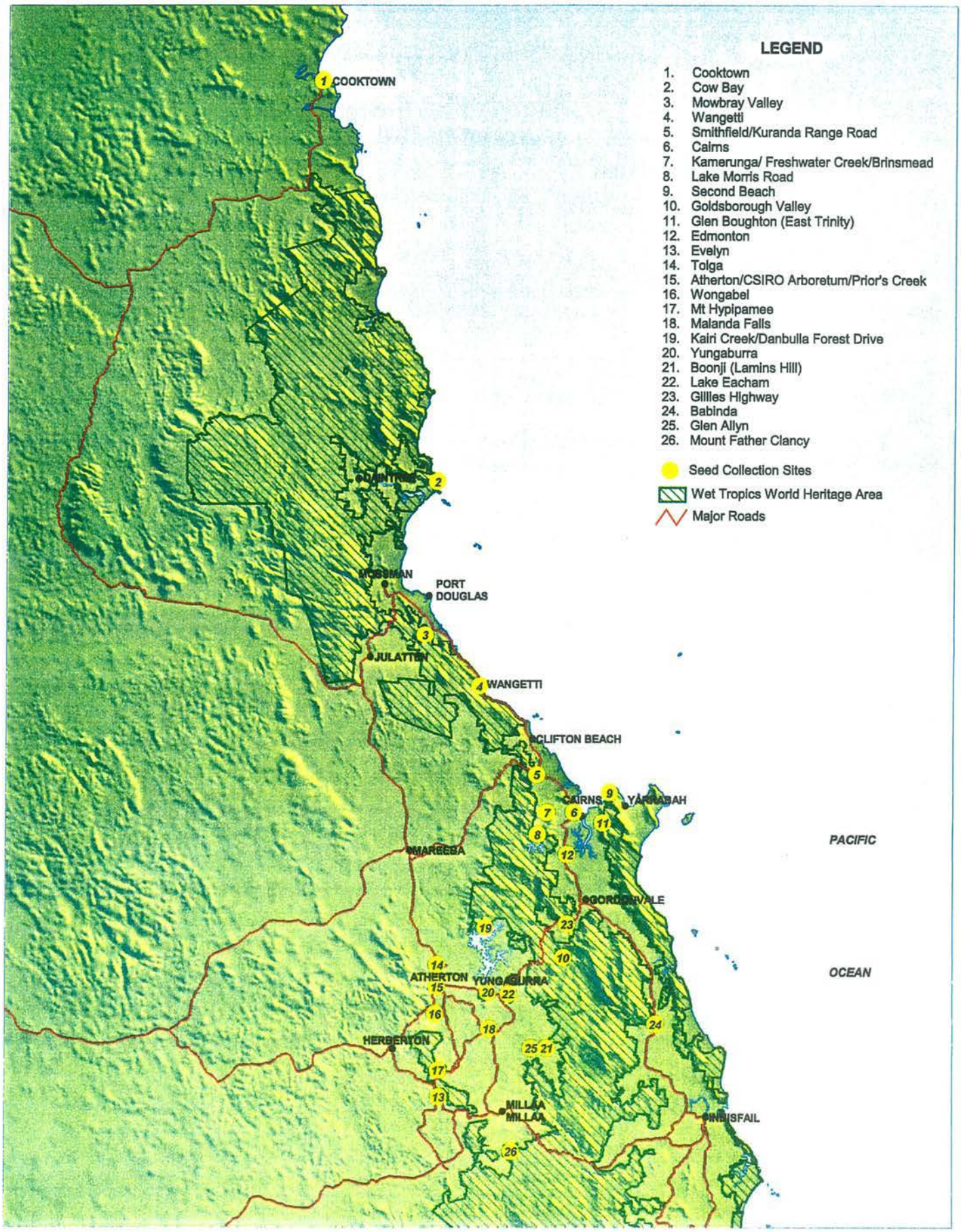
Family	Species name and authority**	Collection site	Date
Agavaceae	*Cordyline cannifolia* R.Br.	Lake Morris Road	3/02/98
Anacardiaceae	*Blepharocarya involucrigera* F.Muell.	Lake Morris Road	19/01/98
Apocynaceae	*Cerbera floribunda* K.Schum.	Cow Bay	1/07/98
	Parsonsia latifolia (Benth.) S.T.Blake	Lamins Hill	1/09/98
Araliaceae	*Mackinlaya macrosciadea* (F.Muell.) F.Muell.	Tolga	27/03/98
	Polyscias australiana (F. Muell.) Philipson	Lake Morris Road	3/01/98
	Polyscias elegans (C.Moore & F.Muell.) Harms	Mowbray Valley	18/05/98
Araucariaceae	*Agathis robusta* (F.Muell.) F.M.Bailey	Prior's Creek	7/01/98
Arecaceae	*Archontophoenix alexandrae* (F.Muell.) H.Wendl.& Drude	CSIRO arboretum	28/10/97
	Arenga australasica (H.L.Wendt & Drude) S.T.Blake	Cairns	20/02/98
	Calamus australis Mart.	Lake Morris Road	4/01/98
	Licuala ramsayi (F.Muell.) Domin	Cairns	20/02/98
	Linospadix minor (W.Hill) F.Muell.	Cairns	20/02/98
	Ptychosperma elegans (R.Br.) Reinw. Ex Blume	Cairns	20/02/98
	Ptychosperma macarthurii (Veitch) Hook. f.	Cairns	2/02/98
	Wodyetia bifurcata A.K.Irvine 1	Kamerunga	18/11/97
	Wodyetia bifurcata A.K.Irvine 2	Edmonton	2/05/98
Boraginaceae	*Cordia dichotoma* G.Forst.	Smithfield	24/01/98
Burseraceae	*Canarium vitiense* A.Gray	Lake Morris Road	23/03/98
Casuarinaceae	*Casuarina equisetifolia* L.	Second Beach	5/05/98
Celestraceae	*Cassine melanocarpa* (F.Muell.) Kuntze	Wangetti	6/04/98
	Maytenus fasciculiflora Jessup	Wangetti	6/04/98
Combretaceae	*Terminalia sericocarpa 1* (F.Muell.)	Cairns	3/01/98
	Terminalia sericocarpa 2 (F.Muell.)	Goldsborough Valley	2/02/98
Convolvulaceae	*Ipomoea hederifolia* L.	Goldsborough Valley	13/07/98
Corynocarpaceae	*Corynocarpus cribbianus* (Bailey) C.T.White ex L.S.Sm.	Malanda Falls	12/01/98
Cucurbitaceae	*Diplocyclos palmatus* (L.) C.Jeffrey	Mowbray Valley	18/05/98
	Trichosanthes pentaphylla Benth.	Mowbray Valley	18/05/98
Cyperaceae	*Gahnia* sp.	Kauri Creek	26/05/98
Dioscoreaceae	*Dioscorea bulbifera* L. var. bulbifera	Goldsborough Valley	13/07/98
Dichapetalaceae	*Dichapetalum papuanum* (Becc.) Boerl.	Goldsborough Valley	10/02/98
Dilleniaceae	*Hibbertia scandens* (Willd.) Dryand.	Lake Morris Road	30/03/98
Elaeagnaceae	*Elaeagnus triflora* Wall ex Roxb.	Evelyn	23/02/98
Euphorbiaceae	*Antidesma erostre* Benth.	Atherton	4/11/98
	Breynia stipitata Mull.Arg.	Cow Bay	20/07/98
	Glochidion philippicum (Cav.) C.B. Rob.	CSIRO arboretum	17/09/98
	Mallotus mollissimus (Geiseler) Airy Shaw	CSIRO arboretum	8/10/98
Eupomatiaceae	*Eupomatia laurina R.Br.*	Lake Morris Road	4/05/98
Fabaceae	*Castanospermum australe* A.Cunn.& C.Fraser ex Hook	Wongabel	17/08/98
	Centrosema pubescens Benth.	Goldsborough Valley	13/07/98
	Sophora tomentosa L.	Atherton	5/11/97
Flacourtaceae	*Casearia* sp.(=RFK/773)	Smithfield	19/05/98
Flagellariaceae	*Flagellaria indica* L.	Lake Morris Road	15/04/98
Goodeniaceae	*Scaevola taccada* Wall ex Roxb.	Cow Bay	20/07/98
Hippocrateaceae	*Salacia chinensis* L.	Cow Bay	1/07/98
Icacinaceae	*Gomphandra australiana* F.Muell.	Lake Morris Road	24/11/97
	Irvingbaileya australis (C.T.White) R.A.Howard	Boonjie	15/09/98
Lauraceae	*Cryptocarya* sp.	Kamerunga	13/11/97
	Cryptocarya clarksoniana B. Hyland	Kamerunga	13/11/97
	Cryptocarya hypospodia 1 F.Muell.	Kamerunga	13/11/97
	Cryptocarya hypospodia 2 F.Muell.	Brinsmead	13/11/97

Family	Species name and authority**	Collection site	Date
Lauraceae	*Cryptocarya mackinnoniana* F.Muell.	Lake Morris Road	21/04/98
	Cryptocarya murrayi F.Muell.	Kamerunga	13/11/97
	Cryptocarya triplinervis var. riparia B.Hyland	Freshwater Creek	24/01/98
	Endiandra insignis (Bailey) F.M.Bailey	Lake Morris Road	14/09/98
	Neolitsea dealbata (R.Br.) Merr.	Lake Eacham	27/03/98
Leeaceae	*Leea indica* Merr.	Lake Morris Road	30/03/98
Meliaceae	*Aglaia sapindina* (F.Muell.) Harms	Goldsborough Valley	10/02/98
Menispermaceae	*Hypserpa laurina 1* (F. Muell.) Diels	Goldsborough Valley	2/02/98
	Hypserpa laurina 2 (F. Muell.) Diels	Lake Morris Road	3/02/98
	Legnephora moorei (F.Muell.) Miers	Lake Morris Road	12/05/98
	Sarcopetalum harveyanum F.Muell.	Boughton Glen	5/05/98
Mimosaceae	*Pararchidendron pruinosum* (Benth.) I.C.Nielsen	Cairns	15/11/98
Moraceae	*Ficus adenosperma* Miq.	CSIRO arboretum	24/09/98
	Trophis scandens (Lour.) Hook & Arn.	Smithfield	16/10/98
Myristicaceae	*Myristica insipida* R.Br.	Lake Morris Road	12/05/98
Myrsinaceae	*Ardisia crispa* (Thunb.) DC. *	Atherton	20/07/98
Myrtaceae	*Acmena graveolens* (Bailey) C.T.White & L.S.Sm.	Babinda	29/09/98
	Acmena hemilampra (F.Muell.) Merr.& L.M.Perry	Cow Bay	1/07/98
	Archirhodomyrtus beckleri (F.Muell.) A.J.Scott	Lake Morris Road	3/02/98
	Decaspermum humile (G.Don) A.J.Scott	Atherton	20/07/98
	Rhodomyrtus pervagata Guymer	Lake Morris Road	4/05/98
	Syncarpia glomulifera (Sm.) Nied.	Lake Morris Road	4/05/98
	Syzygium angophoroides (F.Muell.) B.Hyland	Lake Morris Road	3/02/98
	Syzygium cormiflorum (F.Muell.) B.Hyland	Goldsborough Valley	28/01/98
	Syzygium kuranda (Bailey) B.Hyland	Atherton	26/10/97
	Syzygium luehmannii (F.Muell.) L.A.S.Johnson	Goldsborough Valley	2/02/98
	Syzygium tierneyanum (red) (F.Muell.) T.G.Hartley & L.M.Perry	Freshwater Creek	24/01/98
	Syzygium tierneyanum (white) (F.Muell.) T.G.Hartley & L.M.Perry	Freshwater Creek	24/01/98
Oleaceae	*Chionanthus ramiflorus* Wall.ex Roxb.	Smithfield	18/08/98
	Jasminum didymum G.Forst.	Lake Morris Road	14/09/98
	Ligustrum lucidum Aiton *	Yungaburra	26/08/98
Passifloraceae	*Adenia heterophylla* (Blume) Koord.*ssp heterophylla*	Smithfield	19/05/98
Phytolaccaceae	*Rivina humilis* L. *	Lake Morris Road	9/06/98
Piperaceae	*Piper caninum* Reinw. ex Blume	Lake Morris Road	14/09/98
	Piper macropiper Pennant	Lake Morris Road	9/03/98
	Piper novae-hollandiae Miq.	Lake Morris Road	4/05/98
Pittosporaceae	*Pittosporum* (=RFK/2369)	Evelyn	23/02/98
	Pittosporum sp.	Lake Morris Road	10/01/98
	Pittosporum venulosum F.Muell.	Gillies Lookout Rd	11/05/98
	Pittosporum wingii F.Muell.	Lake Morris Road	9/03/98
Podocarpaceae	*Podocarpus grayae* de Laub.	Lake Morris Road	30/11/98
	Prumnopitys amara 1 (Blume) de Laub	Mt Hypipamee	25/01/98
	Prumnopitys amara 2 (Blume) de Laub	Mt Hypipamee	3/02/98
Proteaceae	*Cardwellia sublimis* F. Muell.	Glen Allyn	22/11/97
	Carnarvonia araliifolia F.Muell.	Lake Morris Road	3/01/98
	Darlingia darlingiana (F.Muell.) L.A.S. Johnson	Atherton	20/01/98
Rhamnaceae	*Colubrina asiatica* (L.) Brongn.	Koombal	5/05/98
Rosaceae	*Prunus turneriana* (Bailey) Kalkman	Mt Father Clancy	16/11/97
Rubiaceae	*Antihrea tenuiflora* F.Muell. Ex Benth.	Lake Morris Road	3/02/98
	Gardenia ovularis F.M.Bailey	Lake Morris Road	9/03/98
	Hodgkinsonia frutescens C.T.White	Wongabel	17/08/98
	Lasianthus strigosus Wight	Lake Morris Road	9/03/98
	Randia sessilis F.Muell.	Cooktown	30/07/98

Family	Species name and authority**	Collection site	Date
Rutaceae	*Evodiella muelleri* (Engl.) B.L.Linden	Smithfield	20/03/98
	Flindersia ifflaiana F. Muell	Lake Morris Road	27/10/97
Rutaceae	*Glycosmis trifoliata* Spreng.	Goldsborough Valley	2/02/98
	Micromelum minutum (G.Forst.) Wight & Arn.	Goldsborough Valley	21/09/98
	Zanthoxylum ovalifolium Wight	Wongabel	27/03/98
Santalaceae	*Dendrotrophe varians* (Blume) Miq.	Goldsborough Valley	21/09/98
Sapindaceae	*Castanospora alphandii* (F.Muell.) F.Muell.	Mt Hypipamee	7/01/98
	Cupianopsis anacardioides (A. Rich.) Radlk.	Cairns	14/11/98
	Diploglottis diphyllostegia (F.Muell.) F.M.Bailey	Yungaburra	5/11/97
	Ganophyllum falcatum Reinw. ex Blume	Smithfield	24/01/98
	Mischocarpus exangulatus (F.Muell.)Radlk.	Boonjie	1/09/98
	Synima cordierorum (F.Muell.) Radlk.	Evelyn	7/01/98
	Toechima erythrocarpum F.Muell.	Kamerunga	23/11/97
	Toechima daemelianum (F.Muell.) Radlk.	Lake Morris Road	13/11/97
Sapotaceae	*Pouteria obovoidea* (H.J. Lam) Baehni	Stoney Creek	25/08/98
Simaroubaceae	*Brucea javanica* (L.) Merr.	Smithfield	21/02/98
Solonaceae	*Solanum seaforthianum* Andrews*	Lake Morris Road	9/06/98
Sterculiaceae	*Argyrodendron* sp.	Lake Morris Road	13/11/97
	Argyrodendron polyandrum 1 C.T.White ex L.S.Sm.	Lake Morris Road	3/01/98
	Argyrodendron polyandrum 2 C.T.White ex L.S.Sm.	Lake Morris Road	3/01/98
Verbenaceae	*Callicarpa pedunculata* R.Br.	Lake Morris Road	23/03/98
	Clerodendrum tracyanum (F.Muell.) Benth.	Lake Morris Road	4/05/98
	Gmelina fasciculiflora 1 Benth.	Cairns	8/01/98
	Gmelina fasciculiflora 2 Benth.	Goldsborough Valley	10/02/98
	Lantana camara 1 L *	Goldsborough Valley	14/07/98
	Lantana camara 2 L *	Smithfield	31/08/98
	Vitex helogiton K.Schum	CSIRO arboretum	8/04/98
Vitaceae	*Tetrastigma nitens* (F.Muell.) Planch	Lake Morris Road	23/03/98
	Tetrastigma thorsborneorum Jackes	Smithfield	24/08/98
Winteraceae	*Bubbia semicarpoides* (F. Muell.) B.L.Burtt	Kuranda Range Rd	24/03/98
Zingiberaceae	*Alpinia arctiflora* (F.Muell.) Benth.	Lake Morris Road	30/03/98
	Alpinia caerulea R.Br.) Benth.	Lake Morris Road	30/03/98
	* introduced species		

**Source Henderson, R. (1997) *Queensland plants. Names and distribution,* Brisbane:Department of Environment.

FIGURE 2.1 SEED COLLECTION LOCATIONS



Speed of germination

Germination in white light was recorded for 112 seedlots representing 106 species. Table 2.2 shows these species grouped according to the time to commencement of germination. Sixty-seven seedlots representing 63 species were early germinators (germination commenced within six weeks of sowing), while a further 26 species were intermediate germinators (germination commenced between seven and 12 weeks). The remaining 19 seedlots (representing 17 species) were late germinators, with some of these seedlots germinating up to 31 weeks after sowing. One species, *Blepharocarya involucrigera*, displayed viviparity, with seeds observed to be already germinating when they were extracted from the involucre of long linear bracts (Hyland and Whiffin, 1993) in which they were borne. A number of species did not germinate in this study even after 12 months, although their seeds appeared intact. These species included *Acmena graveolens, Colubrina asiatica, Dendrotrophe varians, Gahnia* sp., *Irvingbaileya australis, Licuala ramsayi* and *Trichosanthes pentaphylla.*

The total number of species that commenced germinating in each week is summarised in Figure 2.2, while Figure 2.3 shows this data as a cumulative total of the % of species that had germinated by each week. Germination had commenced in 49% of species by 4 weeks after sowing; this figure had risen to 83% of species by 12 weeks. *Cupaniopsis anacardioides, Synima cordierorum* and *Toechima erythrocarpum* are included in the count for week 4. They were first recorded at week 6 after a gap in observations; previous experience with these species suggests week 4 is the most likely week of commencement of germination (personal observation, pilot study).

Table 2.2 Germination groups and time to commencement of germination in white light

Early
up to 6 weeks
WEEK 1
Blepharocarya involucrigera
Cardwellia sublimis
Corynocarpus cribbianus
Darlingia darlingiana
Flindersia ifflaiana
Ganophyllum falcatum
Micromelum minutum
Syncarpia glomulifera
Syzygium cormiflorum
Syzygium tierneyanum(red)
Syzygium tierneyanum(white)

WEEK 2
Agathis robusta
Aglaia sapindina
Antirhea tenuiflora
Argyrodendron polyandrum 1
Argyrodendron polyandrum 2
Carnarvonia araliifolia
Castanospora alphandii
Casuarina equisetifolia
Endiandra insignis
Glycosmis trifoliata
Mischocarpus exangulatus
Pararchidendron pruinosum
Pouteria obovoidea
Randia sessilis
Rivina humilis
Syzygium angophoroides
Syzygium luehmannii
Terminalia sericocarpa 2
Trophis scandens

WEEK 3
Breynia stipitata
Canarium vitiense
Centrosema pubescens
Cryptocarya hypospodia 1
Cryptocarya triplinervis
Ficus adenosperma
Ipomoea hederifolia
Jasminum didymum
Piper novae-hollandiae
Scaevola taccada
Solanum seaforthianum
Terminalia sericocarpa 1

WEEK 4
Alpinia arctiflora
Alpinia caerulea
Archirhodomyrtus beckleri
Calamus australis
Chionanthus ramiflorus
Eupomatia laurina
Gardenia ovularis
Ligustrum lucidum
Piper macropiper
Tetrastigma thorsborneorum

WEEK 5
Acmena hemilampra
Castanospermum australe
Cryptocarya hypospodia 2
Diplocyclos palmatus
Elaeagnus triflora
Evodiella muelleri
Parsonsia latifolia

WEEK 6 or less
Ardisia crispa
Casearia sp(=*RFK/773)*
Hodgkinsonia frutescens
Piper caninum
Podocarpus grayae
*Cupaniopsis anacardioides**
*Synima cordierorum**
*Toechima erythrocarpum**

Intermediate
7-12 weeks
WEEK 7
Bubbia semecarpoides
Dioscorea bulbifera
Vitex helogiton

WEEK 8
Cordyline cannifolia
Lantana camara 1
Salacia chinensis

WEEK 9
Lasianthus strigosus
Ptychosperma macarthurii
Tetrastigma nitens

WEEK 10
Cordia dichotoma
Cryptocarya murrayi
Pittosporum wingii
Prunus turneriana

WEEK 11
Antidesma erostre
Archontophoenix alexandrae
Gmelina fasciculiflora 1
Gomphandra australiana
Mackinlaya macrosciadea
Sophora tomentosa
Syzygium kuranda

WEEK 12
Cryptocarya clarksoniana
Dichapetalum papuanum
Diploglottis diphyllostegia
Mallotus mollissimus
Ptychosperma elegans
Rhodomyrtus pervagata

Late
>12 weeks

Adenia heterophylla
Arenga australisica
Callicarpa pedunculata
Cerbera floribunda
Clerodendrum traceyanum
Decaspermum humile
Gmelina fasciculiflora 2
Hibbertia scandens
Hypserpa laurina 1
Hypserpa laurina 2
Leea indica
Legnephora moorei
Linospadix minor
Maytenus fasciculiflora
Neolitsea dealbata
Pittosporum venulosum
Prumnopitys amara 1
Prumnopitys amara 2
Sarcopetalum harveyanum

* first observation in week 6, probably germinated in week 4

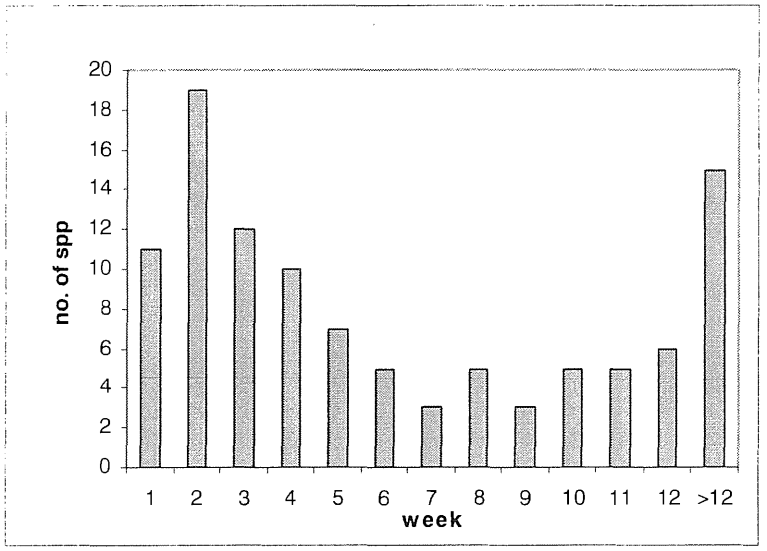


Figure 2.2 Number of species commencing germination in white light by week

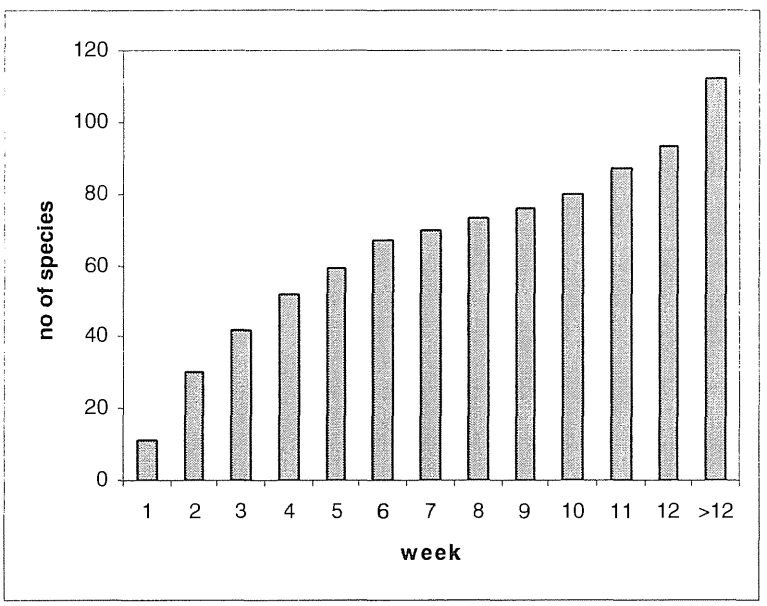
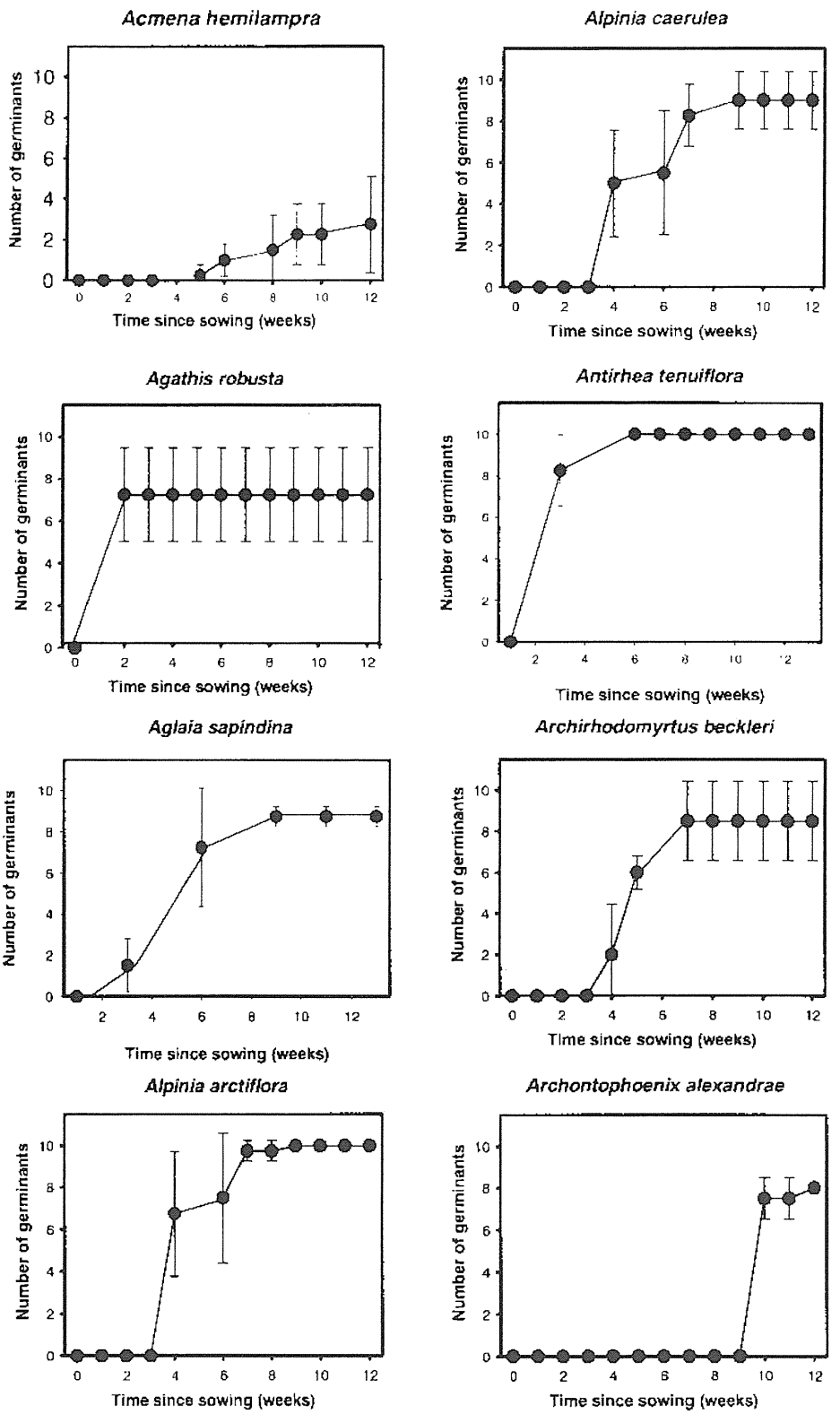


Figure 2.3 Cumulative total of species germinating by week

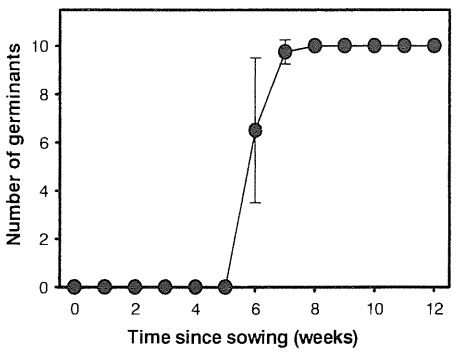
Uniformity and capacity of germination

The pattern of germination over time, the uniformity of germination and the 'germination capacity' (*sensu* Bewley and Black 1994) of each individual species are illustrated in Figure 2.4.

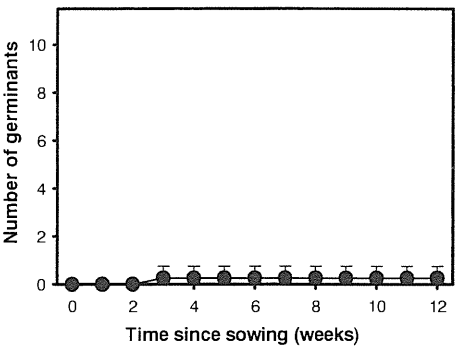
Figure 2.4. Germination over time, showing uniformity and capacity of germination.
Data are presented as means and standard deviations at each measurement time.



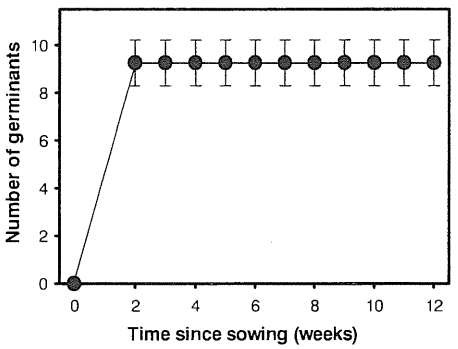
Ardisia crenata



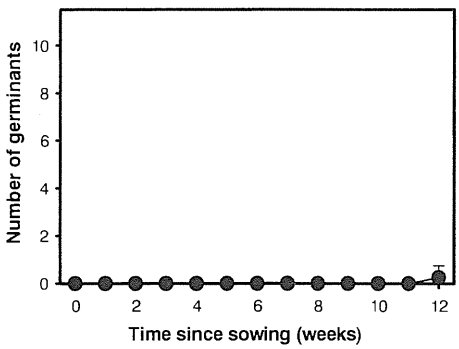
Breynia stipitata



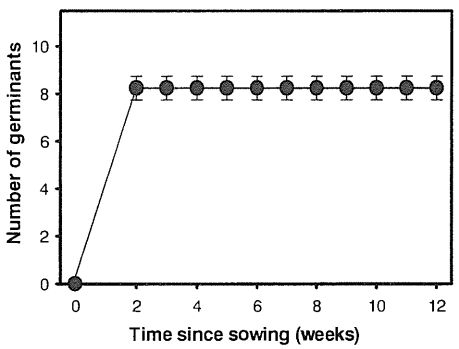
Argyrodendron polyandrum 1



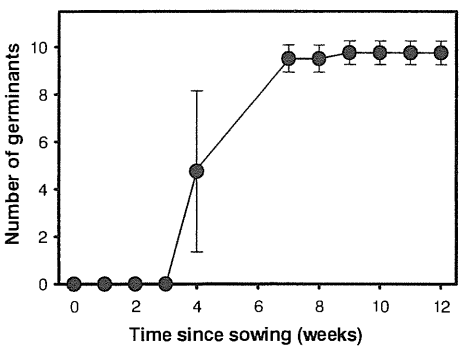
Bubbia semicarpoides



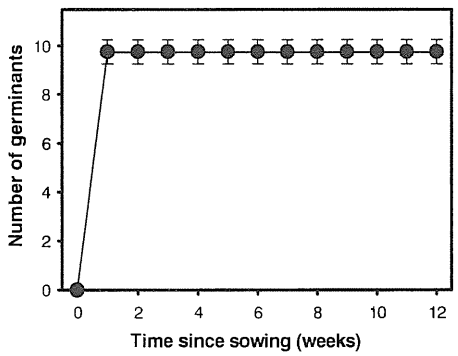
Argyrodendron polyandrum 2



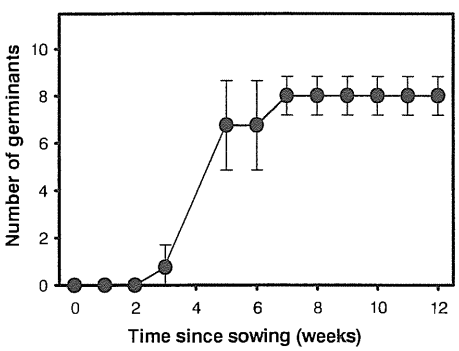
Calamus australis



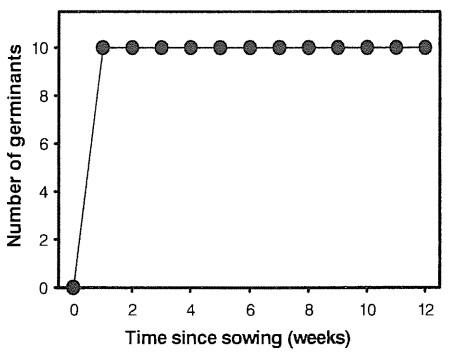
Blepharocarya involucrigera



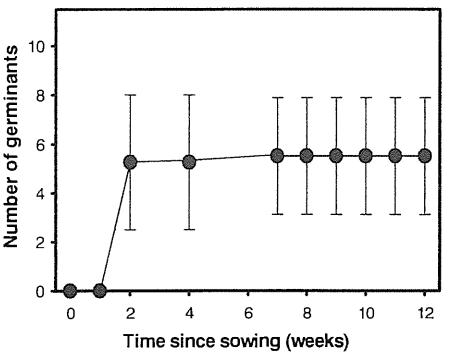
Canarium vitiense



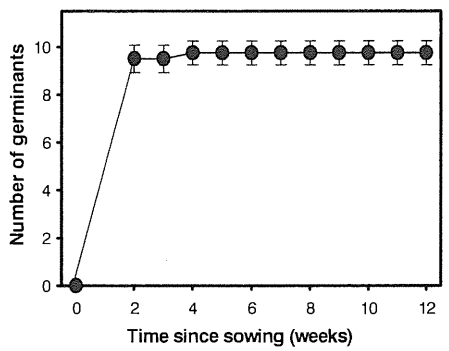
Cardwellia sublimis



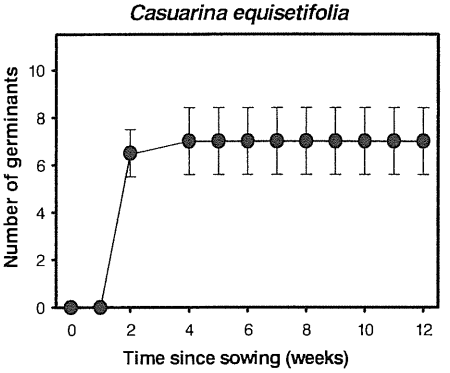
Castanospora alphandii



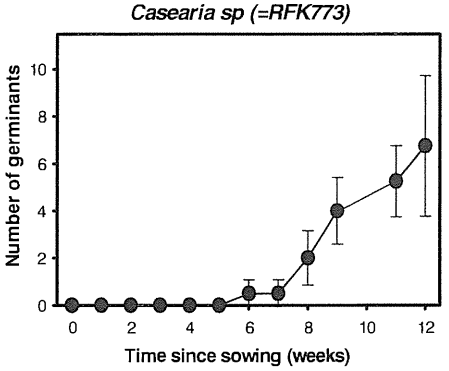
Carnarvonia araliifolia



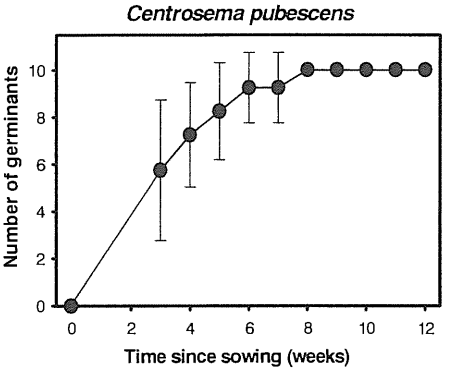
Casuarina equisetifolia



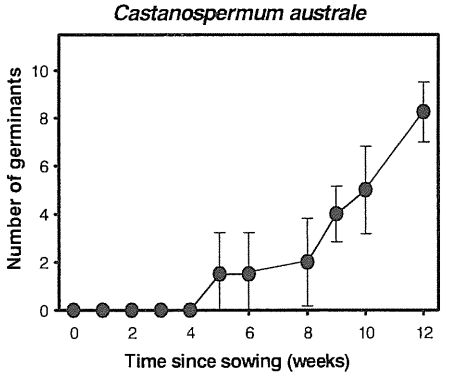
Casearia sp (=RFK773)



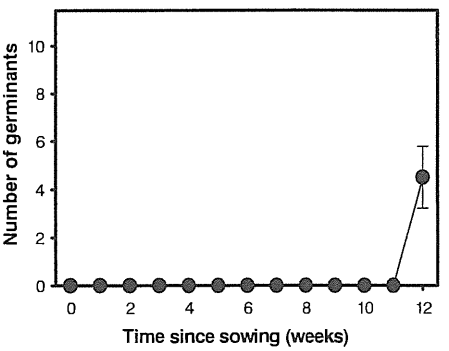
Centrosema pubescens



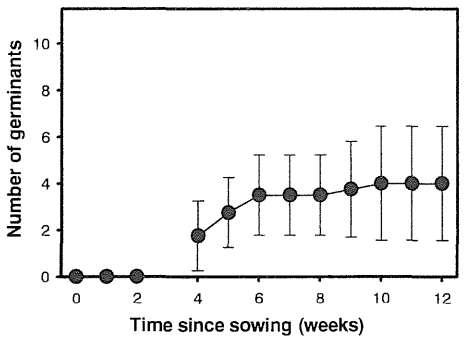
Castanospermum australe



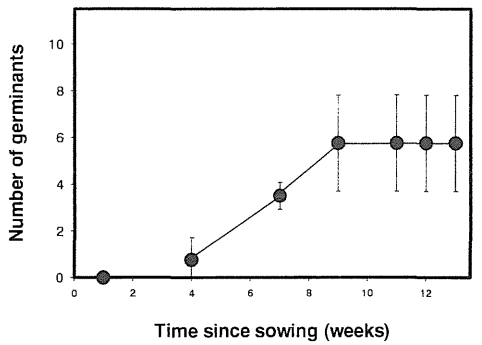
Cerbera floribunda



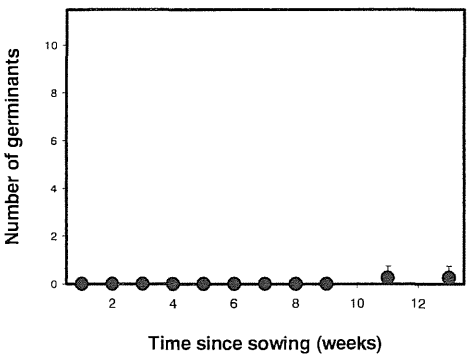
Chionanthus ramiflora



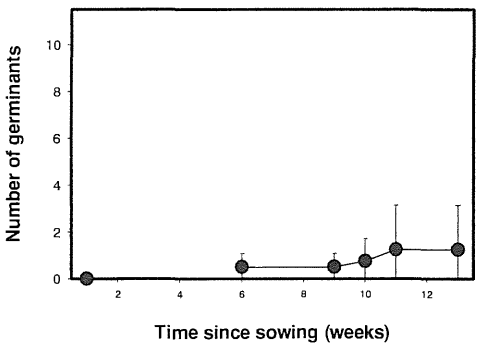
Cryptocarya hypospodia 1



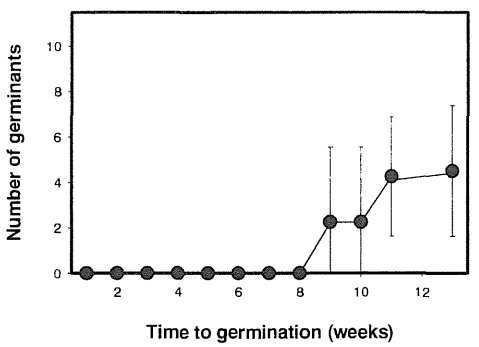
Cordia dichotoma



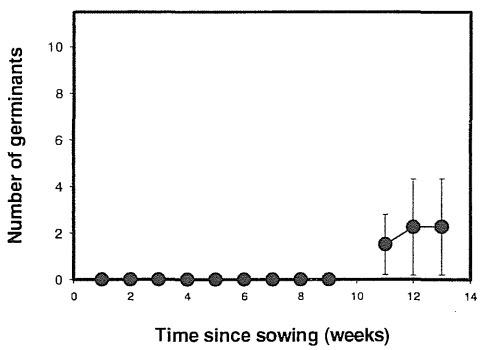
Cryptocarya hypospodia 2



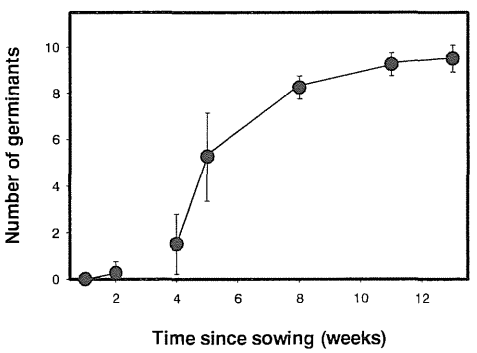
Cordyline cannifolia



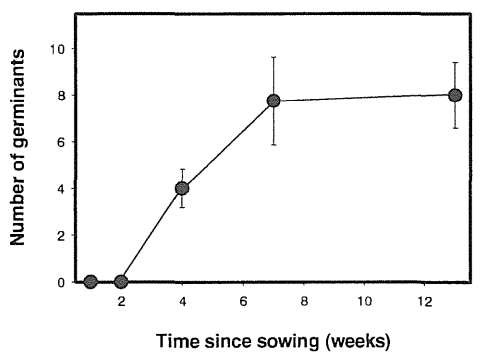
Cryptocarya murrayi



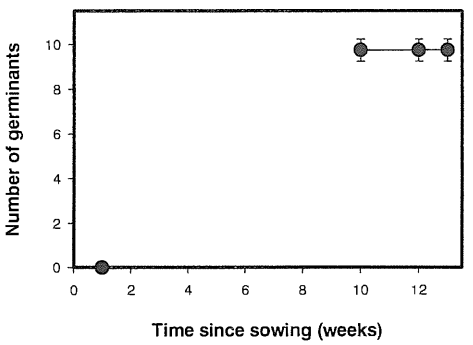
Corynocarpus cribbianus



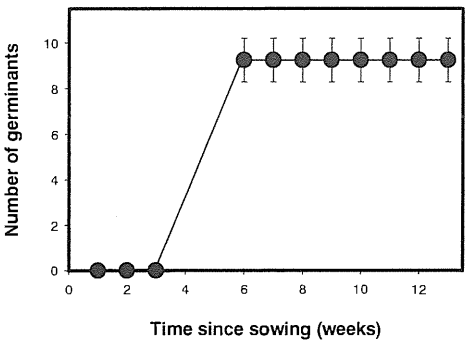
Cryptocarya triplinervis



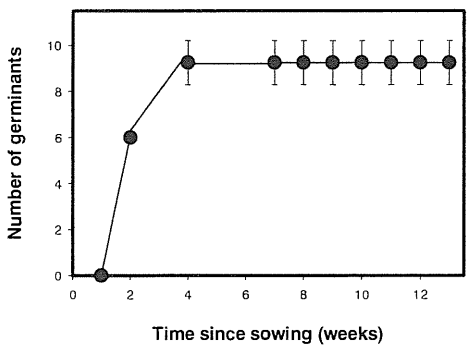
Cupaniopsis anarcardioides



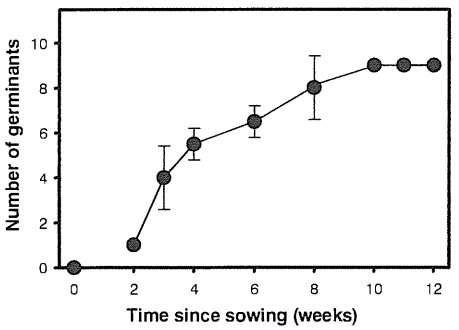
Elaeagnus triflora



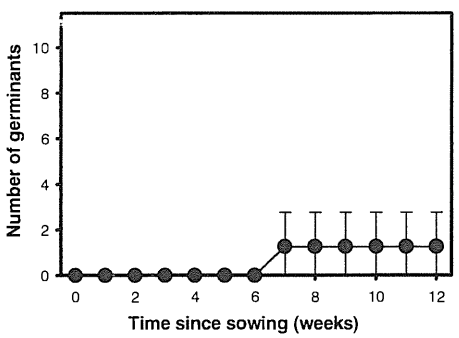
Darlingia darlingiana



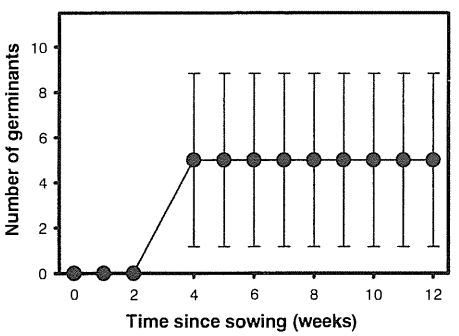
Endiandra insignis



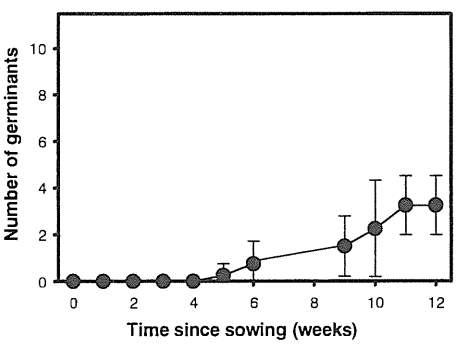
Dioscorea bulbifera



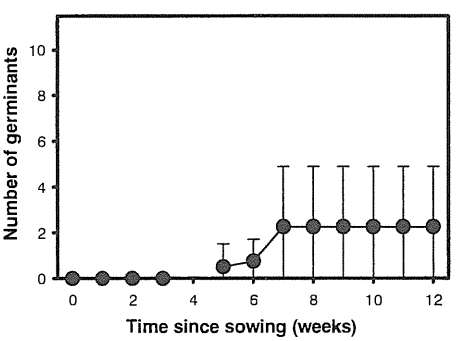
Eupomatia laurina



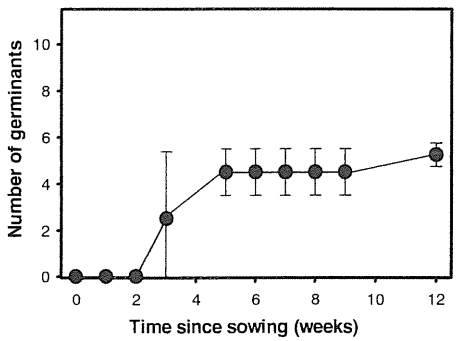
Diplocyclos palmatus



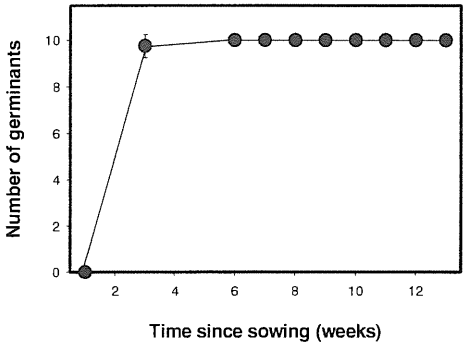
Evodiella muelleri



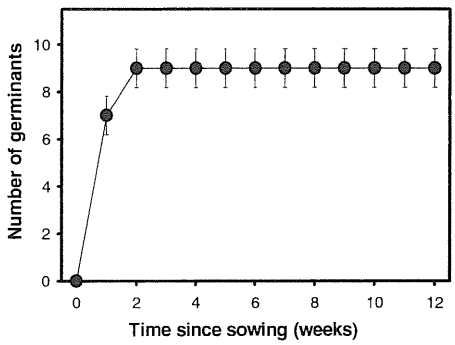
Ficus adenosperma



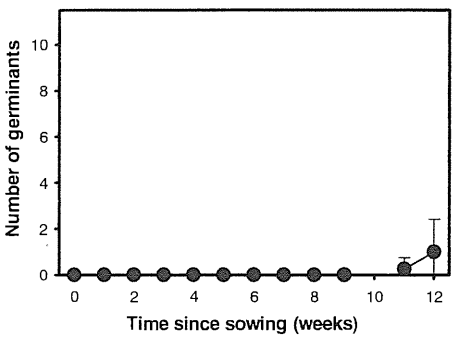
Glycosmis trifoliata



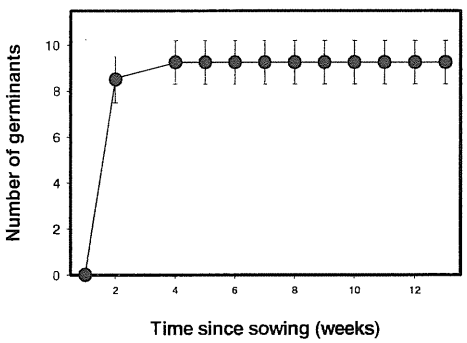
Flindersia ifflaiana



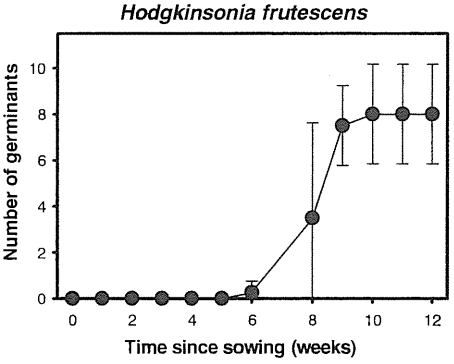
Gomphandra australiana



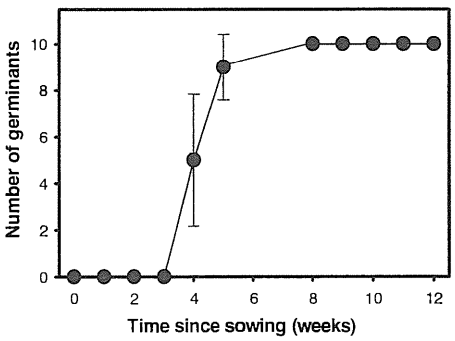
Ganophyllum falcatum



Hodgkinsonia frutescens



Gardenia ovularis



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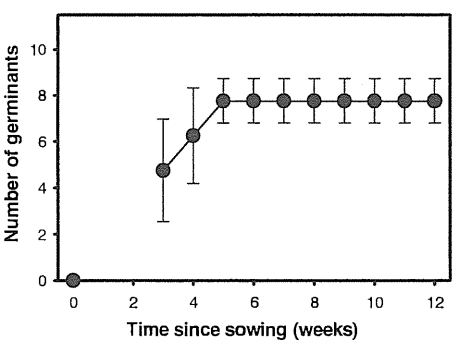

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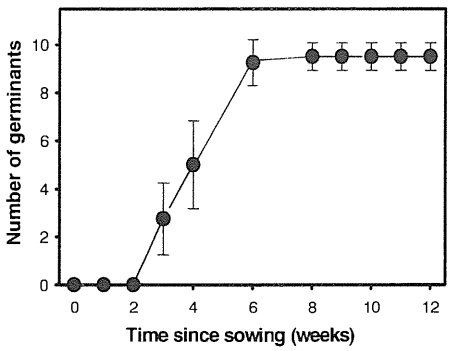

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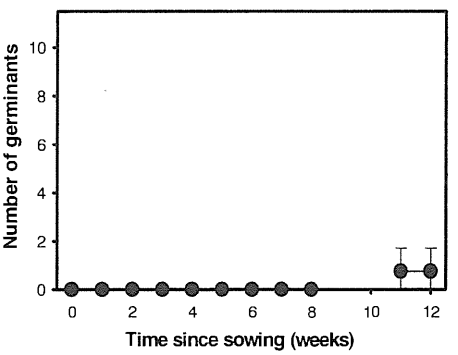

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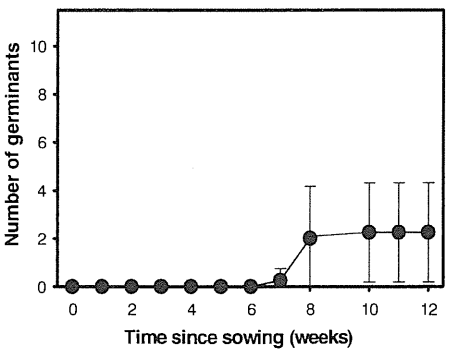

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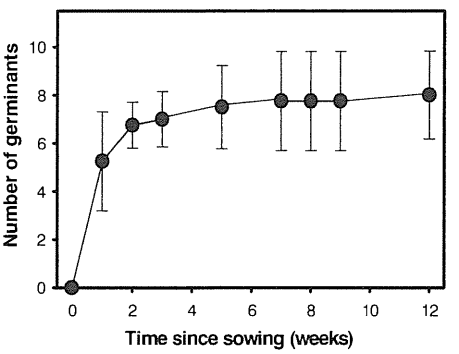

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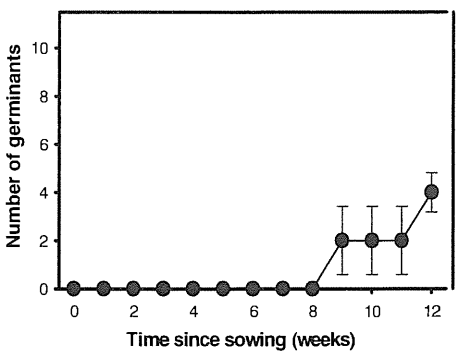

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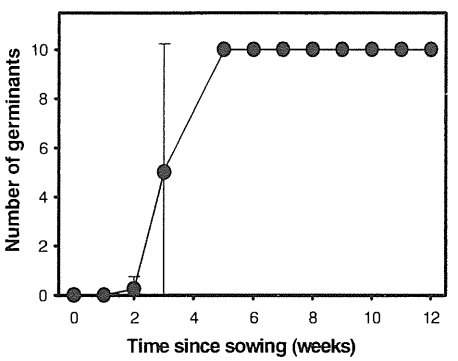

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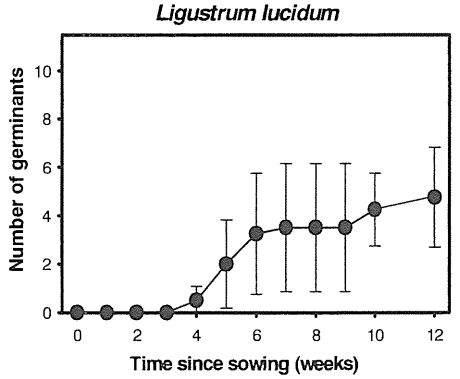

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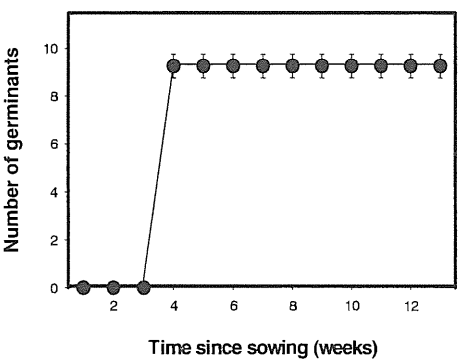

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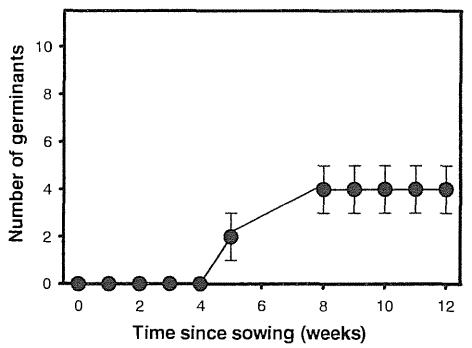

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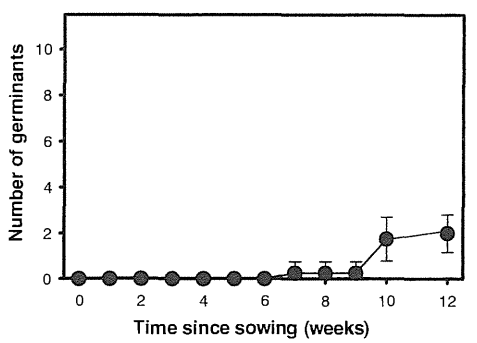
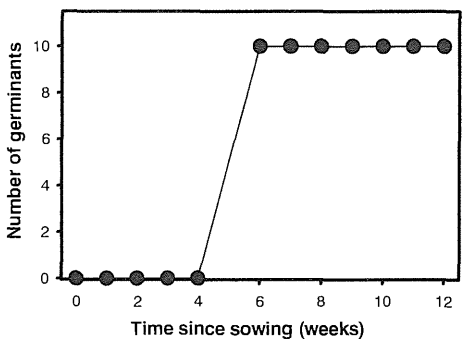
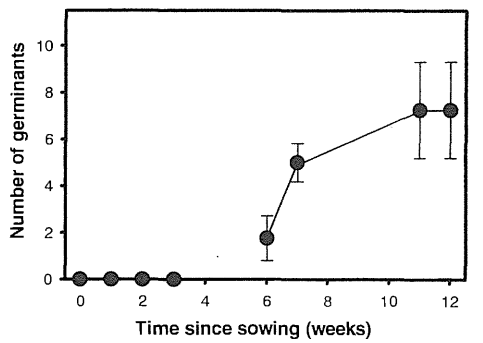


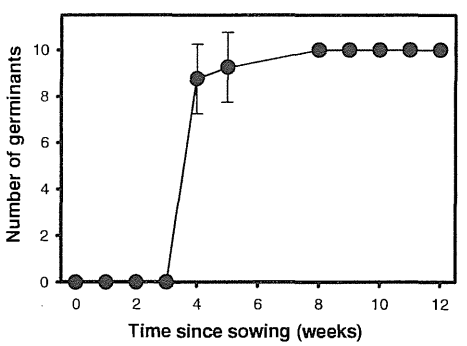
Piper caninum



Podocarpus grayae



Piper macropiper



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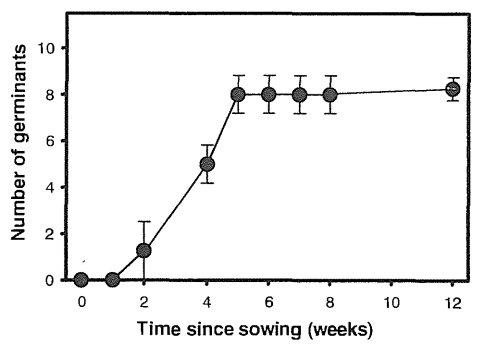

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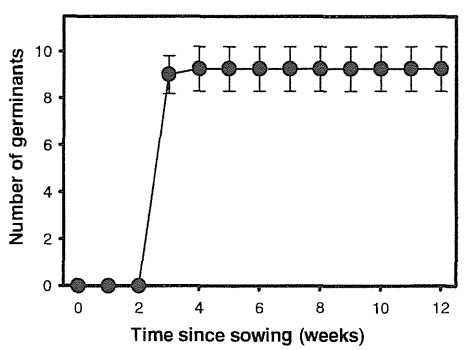

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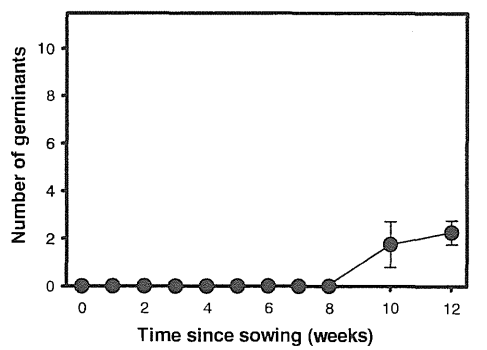

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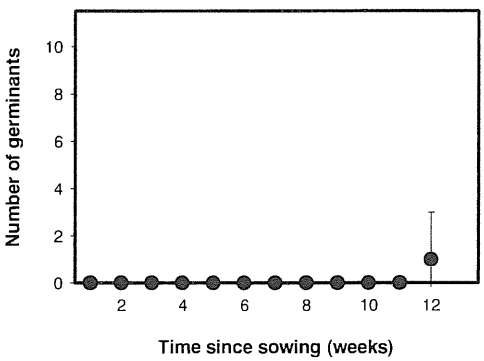
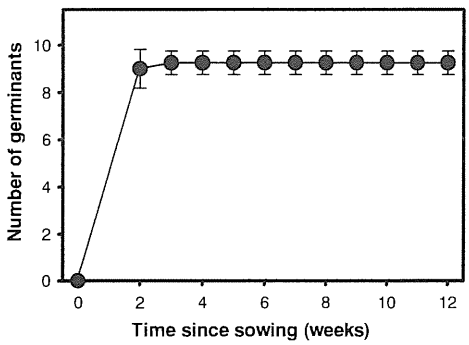
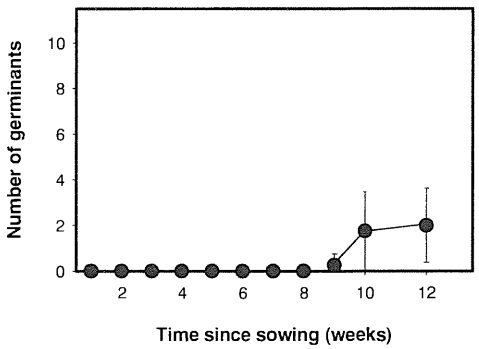


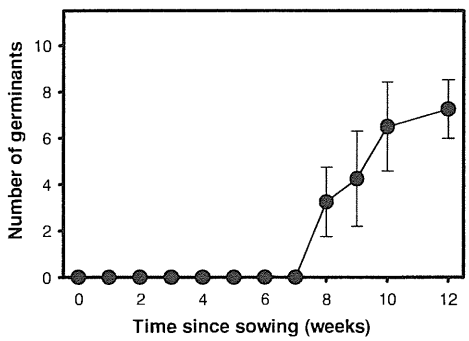
Rivina humilis



Ptychosperma macarthurii



Salacia chinensis



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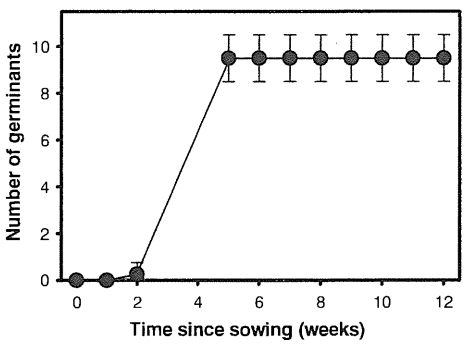
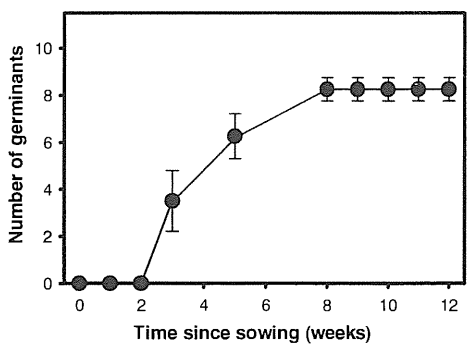
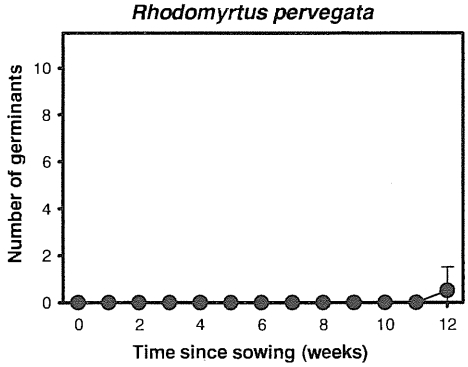


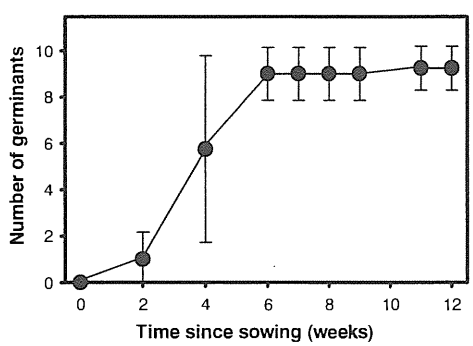
Scaevola taccada



Rhodomyrtus pervegata



Solanum seaforthianum



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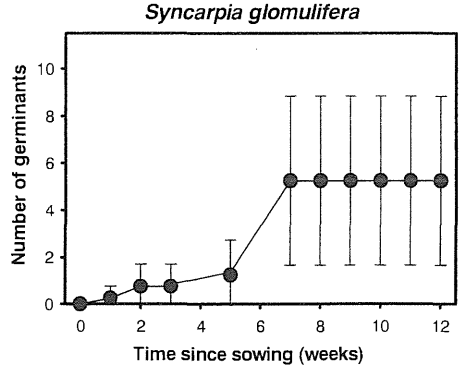
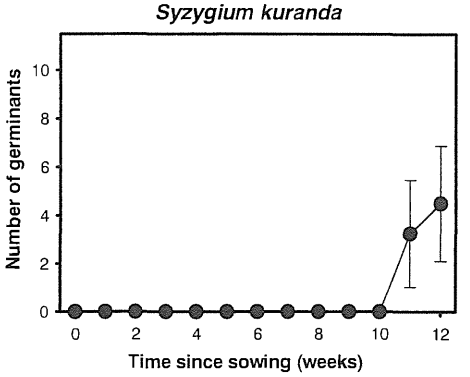
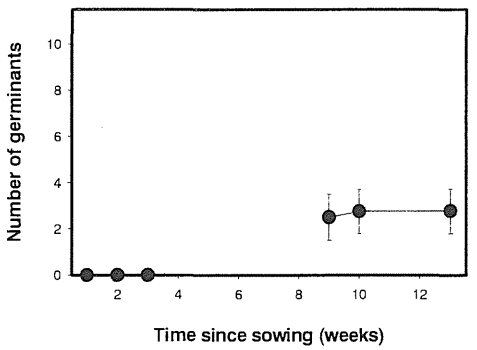


Syzygium kuranda



Synima cordierorum



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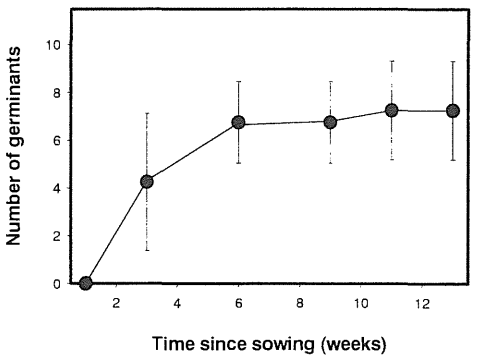
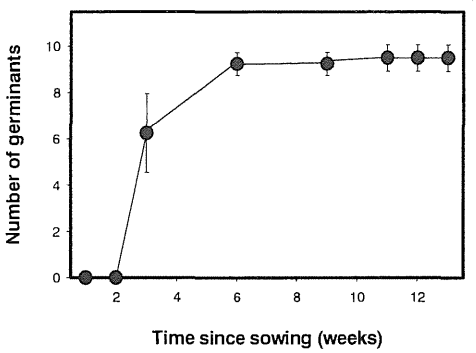
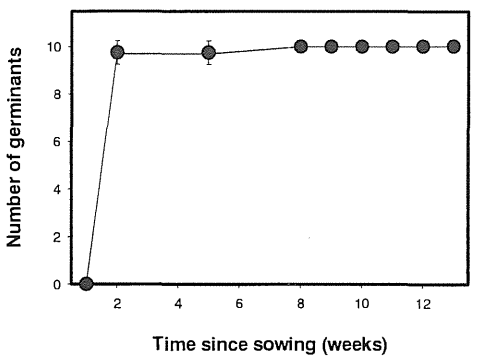


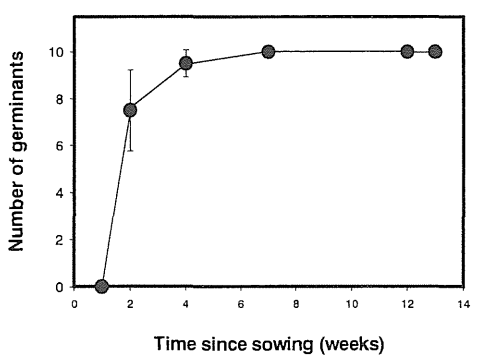
Syzygium angophoroides



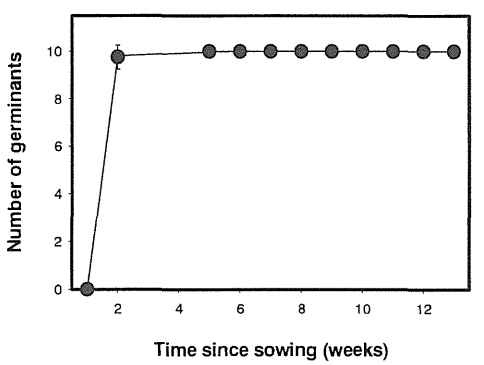
Syzygium tierneyanum (red)



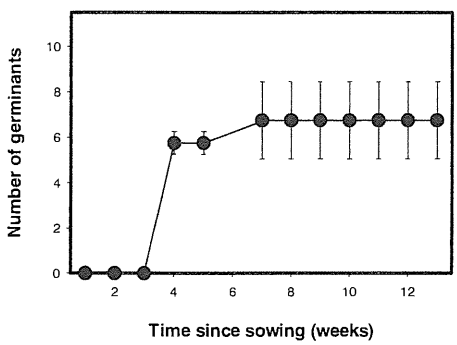
Syzygium cormiflorum



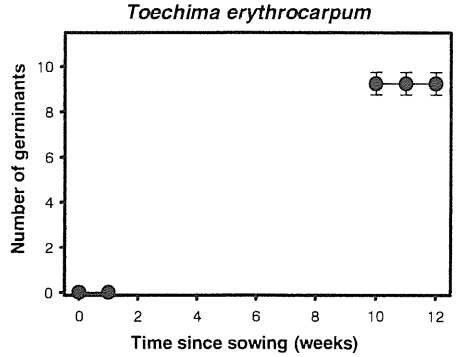
Syzygium tierneyanum (white)



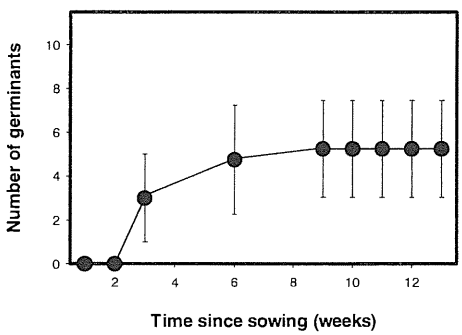
Terminalia sericocarpa 1



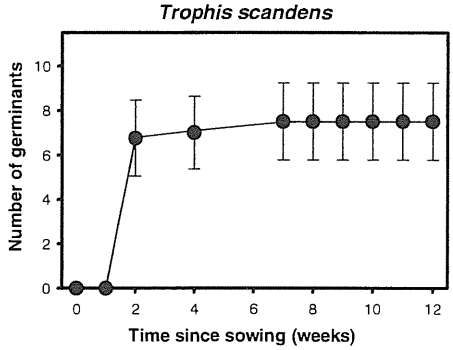
Toechima erythrocarpum



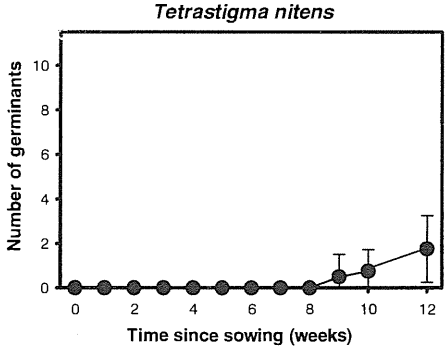
Terminalia sericocarpa 2



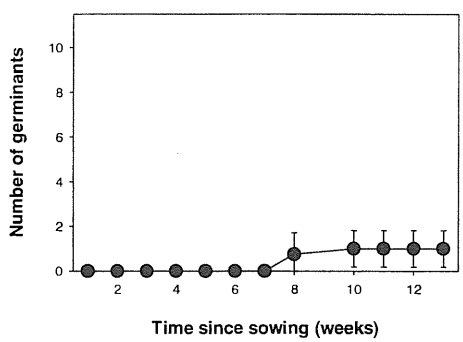
Trophis scandens



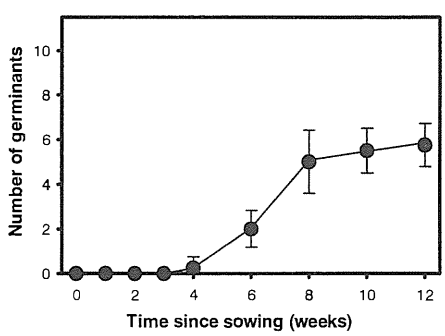
Tetrastigma nitens



Vitex helogiton



Tetrastigma thorsborneorum



Seventy six seedlots had commenced germination by nine weeks after sowing and were considered in the assessment of uniformity of germination. Twenty seven seedlots (36% of those assessed) displayed a high level of uniformity of germination under the conditions of this study. This was characterised by a steeply climbing curve (defined here as one rising from zero or one germinant(s) to close to maximum germination in the space of three weeks) in Figure 2.4. These species were:

Archontophoenix alexandrae
Agathis robusta
Ardisia crenata
Argyrodendron polyandrum 1 and 2
Blepharocarya involucrigera
Cardwellia sublimis
Carnarvonia araliifolia
Castanospora alphandii
Casuarina equisetifolia
Darlingia darlingiana
Elaeagnus triflora
Eupomatia laurina
Flindersia ifflaiana
Ganophyllum falcatum
Gardenia ovularis
Glycosmis trifoliata
Mischocarpus exangulatus
Pararachidendron pruinosum
Piper caninum
Piper macropiper
Piper novae-hollandiae
Randia sessilis
Rivina humilis
Syzygium tierneyanum (red and white)
Trophis scandens

All commenced germination within the first 6 weeks after sowing (*i.e.* they were rapid germinators). The relationship between uniformity and speed of germination for these species is summarised in Figure 2.5. More than 60% of the seedlots that commenced germinating in the first two weeks after sowing displayed highly uniform germination. For species commencing germination in the subsequent four weeks, this value fell to 28% of the total for that period.

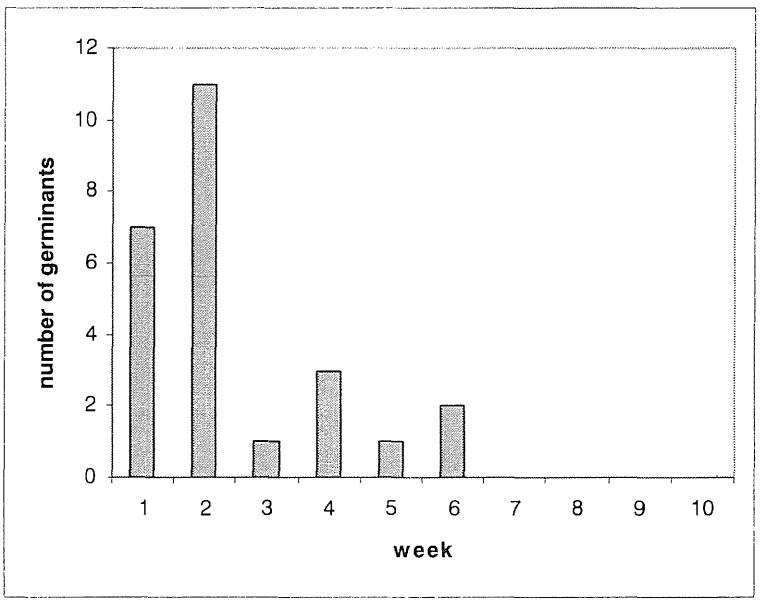


Figure 2.5 Weekly number of germinants with high uniformity of germination

Germination capacity, the proportion of seeds capable of germination under the experimental conditions, was very variable between species that had germinated by the end of the first 12 weeks of this study (Table 2.3). At the upper limit, germination capacity of between 90 and 100% was found for 33 seedlots whilst at the lower limit 14 species had an 'apparent' germination capacity of 10% or less. Caution is required in interpreting this data, especially for those species that are ranked as having low germination capacity but did not commence germination until the later weeks of the study.

The relationship between germination capacity and speed of germination is shown in Figure 2.6.

Table 2.3 Species listed according to germination capacity in white light

Time to commencement of germination in white light is also shown

Species	Germ. Cap. (%)	Week of germination	Species	Germ. Cap. (%)	Week of germination
Alpinia arctiflora	100	4	*Podocarpus grayae*	73	6
Antirhea tenuiflora	100	2	*Salacia chinensis*	73	8
Ardisia crispa	100	6	*Syzygium luehmannii*	73	2
Cardwellia sublimis	100	1	*Casuarina equisetifolia*	70	2
Centrosema pubescens	100	3	*Casearia* sp*(=RFK/773)*	68	6
Gardenia ovularis	100	4	*Terminalia sericocarpa 1*	68	3
Glycosmis trifoliata	100	2	*Cryptocarya hypospodia 1*	58	3
Mischocarpus exangulatus	100	2	*Tetrastigma thorsborneorum*	58	4
Piper caninum	100	6	*Castanospora alphandii*	55	2
Piper macropiper	100	4	*Ficus adenosperma*	53	3
Syzygium cormiflorum	100	1	*Syncarpia glomulifera*	53	1
Syzygium tierneyanum(red)	100	1	*Terminalia sericocarpa 2*	53	2
Syzygium tierneyanum(white)	100	1	*Eupomatia laurina*	50	4
Blepharocarya involucrigera	98	1	*Ligustrum lucidum*	48	4
Calamus australis	98	4	*Syzygium kuranda*	45	11
Carnarvonia araliifolia	98	2	*Cordyline cannifolia*	43	8
Cupianopsis anacardioides	98	4	*Chionanthus ramiflorus*	40	4
Corynocarpus cribbianus	95	1	*Lasianthus strigosus*	40	9
Jasminum didymum	95	3	*Parsonsia latifolia*	40	5
Randia sessilis	95	2	*Acmena hemilampra*	33	5
Syzygium angophoroides	95	2	*Diplocyclos palmatus*	33	5
Argyrodendron polyandrum 1	93	2	*Synima cordierorum*	28	4
Darlingia darlingiana	93	1	*Cryptocarya murrayi*	23	10
Elaeagnus triflora	93	5	*Evodiella muelleri*	23	5
Ganophyllum falcatum	93	1	*Lantana camara*	23	8
Pararchidendron pruinosum	93	2	*Prunus turneriana*	23	10
Piper novae-hollandiae	93	3	*Ptychosperma macarthurii*	20	9
Rivina humilis	93	2	*Pittosporum wingii*	18	10
Solanum seaforthianum	93	3	*Sophora tomentosa*	18	11
Toechima erythrocarpum	93	4	*Tetrastigma nitens*	18	9
Alpinia caerulea	90	4	*Cryptocarya hypospodia 2*	13	5
Endiandra insignis	90	2	*Dioscorea bulbifera*	13	7
Flindersia ifflaiana	90	1	*Cerbera floribunda*	10	13
Aglaia sapindina	88	2	*Gomphandra australiana*	10	11
Archirhodomyrtus beckleri	85	4	*Ptychosperma elegans*	10	12
Argyrodendron polyandrum 2	83	2	*Vitex helogiton*	10	7
Castanospermum australe	83	5	*Mackinlaya macrosciadea*	8	11
Pouteria obovoidea	83	2	*Rhodomyrtus pervegata*	5	12
Scaevola taccada	83	3	*Breynia stipitata*	3	3
Archontophoenix alexandrae	80	11	*Bubbia semecarpoides*	3	7
Canarium vitiense	80	3	*Cordia dichotoma*	3	10
Cryptocarya triplinervis	80	3	*Cryptocarya clarksoniana*	3	12
Hodgkinsonia frutescens	80	6	*Dichapetalum papuanum*	3	12
Micromelum minutum	80	1	*Diploglottis diphyllostegia*	3	12
Ipomoea hederifolia	78	3	*Gmelina fasciculiflora 1*	3	11
Trophis scandens	75	2	*Mallotus mollissimus*	3	12
Agathis robusta	73	2			

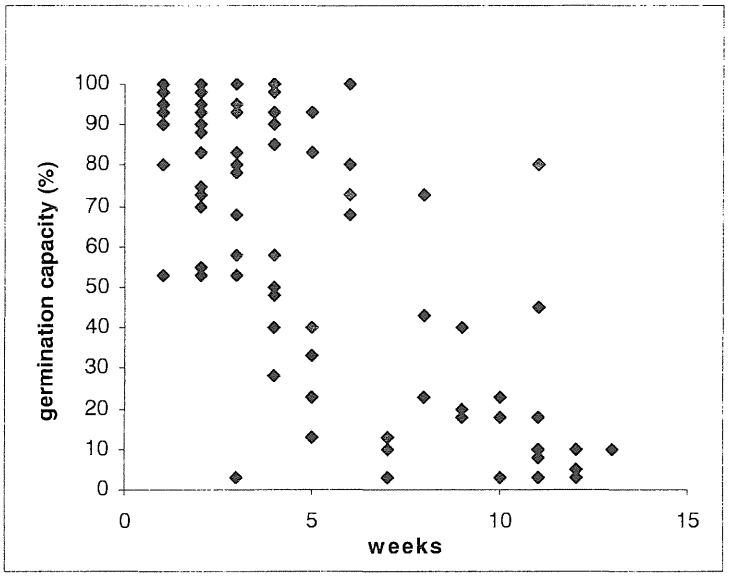


Figure 2.6 Germination capacity and week of germination

High germination capacity is seen to be more common in early germinating species, but species with differential dormancy are not included in this figure. Spearman's correlation coefficient = –0.684 ($p<.001$), indicating a negative relationship between week of germination and germination capacity. Some species might have reached maximum germination after the conclusion of observations. Forty six seedlots (51% of the assessable species) had a high germination capacity, defined here as 75% or greater. A further 14 seedlots (15%) achieved an intermediate level of germination capacity, defined as 50-74%, while the remaining 33 seedlots had low capacity. In all, 66% of seedlots had a germination capacity of 50% or more, and only two species, *Archontophoenix alexandrae* and *Salacia chinensis* in this group of 60 species were not rapid germinators.

Of the 33 seedlots with low germination capacity, only 10 commenced germination in the first six weeks after sowing. The remaining species germinated between seven and 12 weeks.

Table 2.4 shows species grouped according to level of uniformity and germination capacity. High uniformity and high capacity, associated with rapid germination, is seen to be the most common strategy, while slower germination associated with low levels of uniformity and capacity is seen as a more uncommon strategy. Ninety six

percent of the species with a high level of uniformity of germination and high germination capacity were rapid germinators, and this declined to 50% of species with non-uniform germination and low germination capacity. Species with a high level of uniformity of germination invariably had high or intermediate germination capacity.

Two of the largest seeds in this study, *Castanospermum australe* and *Endiandra insignis* had low uniformity of germination associated with high germination capacity, likely a reflection of their ability to persist over time because of nutrient reserves (Kitajima 1996).

Table 2.4 Species grouped according to uniformity and capacity of germination
Species with rapid germination (up to six weeks) are underlined

High uniformity of germination		
high capacity	**intermediate capacity**	**low capacity**
Archontophoenix alexandrae	*Agathis robusta*	
Ardisia crispa	*Castanospora alphandii*	
Argyrodendron polyandrum 1	*Casuarina equisetifolia*	
Argyrodendron polyandrum 2	*Eupomatia laurina*	
Blepharocarya involucrigera		
Cardwellia sublimis		
Carnarvonia araliifoia		
Castanospora alphandii		
Darlingia darlingiana		
Elaeagnus triflora		
Flindersia ifflaiana		
Ganophyllum falcatum		
Gardenia ovularis		
Glycosmis trifoliata		
Mischocarpus exangulatus		
Pararchidendron pruinosum		
Piper caninum		
Piper macropiper		
Piper novae-hollandiae		
Randia sessilis		
Rivina humilis		
Syzygium tierneyanum (red)		
Syzygium tierneyanum (white)		
Trophis scandens		
Intermediate uniformity of germination		
high capacity	**intermediate capacity**	**low capacity**
Aglaia sapindina	*Ipomoea hederifolia*	*Evodiella muelleri*
Alpinia arctiflora	*Podocarpus grayae*	*Ptychosperma macarthurii*
Alpinia caerulea	*Salacia chinensis*	
Archirhodomyrtus beckleri	*Syzygium luehmannii*	
Calamus australis	*Terminalia sericocarpa 1*	
Canarium vitiense	*Terminalia sericocarpa 2*	
Centrosema pubescens		
Hodgkinsonia frutescens		
Jasminum didymum		
Micromelum minutum		
Pouteria obovoidea		
Scaevola taccada		
Solanum seaforthianum		
Non-uniform germination		
high capacity	**intermediate capacity**	**low capacity**
Castanospermum australe	*Casearia* sp	*Acmena hemilampra*
Corynocarpus cribbianus	*Cryptocarya hypospodia 1*	*Chionanthus ramiflorus*
Cryptocarya triplinervis	*Syncarpia glomulifera*	*Cryptocarya hypospodia 2*
Endiandra insignis	*Tetrastigma thorsborneorum*	*Cryptocarya murrayi*
		Diplocyclos palmatus
		Lasianthus strigosus
		Ligustrum lucidum
		Pittosporum wingii
		Prunus turneriana
		Tetrastigma nitens

Of the 67 species for which uniformity and capacity of germination could be assessed, all but eight were rapid germinators. Six of the slower germinating species simultaneously displayed low uniformity and low capacity of germination. Twenty eight per cent of all species had high uniformity of germination, 21% intermediate, and 18% low uniformity. Within these three groups, the proportions of high, intermediate and low capacity vary as shown in Table 2.5.

Table 2.5 Germination capacity groups as a percentage of total germinants in each level of uniformity of germination

	Germination capacity		
Uniformity of germination	high	intermediate	low
high	86	14	0
intermediate	62	29	9
low	22	22	56

A chi square test of independence showed that uniformity of germination is not independent of germination capacity ($\chi^2 = 28.5$, $p<0.001$).

Samaras

Table 2.6 Time and maximum germination for samaras

Species name	Weeks to maximum germination	Maximum percent germination achieved
Agathis robusta	2	73
Argyrodendron polyandrum 1	2	93
Argyrodendron polyandrum 2	2	83
Cardwellia sublimis	1	100
Carnarvonia araliifolia	4	98
Casuarina equisetifolia	4	70
Darlingia darlingiana	3	93
Flindersia ifflaiana	2	90

All the samaras included in the study germinated rapidly, with high uniformity and capacity in excess of 70% (Table 2.6). The wind dispersed seeds of *Blepharocarya involucrigera* responded in the same way.

In contrast to the group above, there are no wind dispersed propagules in the intermediate and non-uniform germination groups. (Two other wind dispersed species, *Parsonsia latifolia* and *Dioscorea bulbifera,* could not be assessed for uniformity, but had rapid/intermediate capacity germination and intermediate/low capacity germination respectively).

2.4 Discussion

In this first comprehensive study of the germination behaviour of over one hundred Australian tropical rainforest species, it was found that seeds of the majority of species germinated within six weeks of sowing. This is consistent with findings reported from studies in other tropical rainforests (*e.g.* Ng 1973, Garwood 1983, Miquel 1987). In addition to investigating the speed of germination, uniformity and capacity of germination were also examined. A high level of uniformity of germination and high germination capacity were found to be common in species that germinated within the first six weeks after sowing. Combining speed, uniformity and capacity, new germination response groups were suggested.

Time to commencement of germination

In some instances, the time taken for initiation of germination in this study differs from that recorded by others. Of the 112 seed lots for which time to commencement of germination was recorded, 60% were early germinators, 23% intermediate germinators and 17% late germinators. For the 73 woody species the relative percentages were 66%, 22% and 12%. These data are comparable to the results reported for germination of woody species in Malaysia (Ng 1980) and Gabon (Miquel 1987). Ng found that 66% of 335 woody species commenced germination within six weeks, and Miquel reported a similar proportion for 105 species in Gabon. Figure 2.7 shows the percentages of fast and slow germinating species in these three areas.

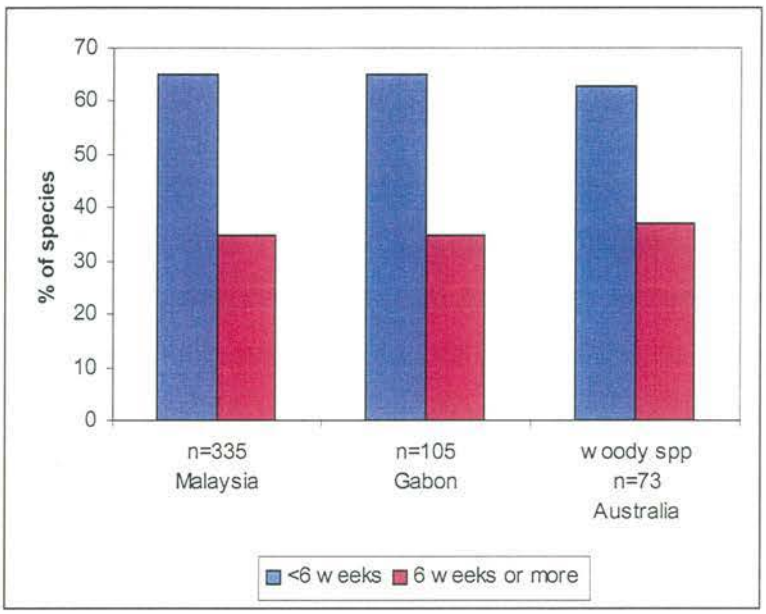


Figure 2.7 Proportions of fast and slow germinators in three tropical rainforests

It seems the germination cues of tropical rainforests and the response of seeds of tropical rainforest woody species interact in similar ways in at least the Malaysian, Gabonese and Queensland situations, and possibly in other locations as well. Garwood (1996) reported a similar situation in a study of abundance of five seedling types in samples from eight tropical forests on three continents. These results suggest similar selective pressures are operating and producing similar responses in all these tropical rainforest areas.

As mentioned above, when all life forms are included the percentage of early germinators declined, suggesting different responses to germination cues in non-tree species. It would be of interest to study germination patterns over time for all lifeforms and in other tropical rainforests, especially those of Papua New Guinea, where a mixture of Australian and Malaysian species occur.

Germination strategies

Speed, uniformity and capacity of germination

The germination strategy of species in the group with rapid germination, high uniformity and high capacity of germination could be regarded as saturation reproduction which depends on the chance of some offspring surviving the hazards of competition, disease and predation to become established in the forest. The

vulnerability of seedlings to parasitism and predation has been reported to be less than that of dormant seeds (Vasquez-Yanes and Orozco-Segovia 1993) – an additional advantage of rapid germination.

The high proportion of species with rapid germination accompanied by high uniformity and capacity of germination is indicative of the success of this as a germination strategy. Low germination capacity is unrepresented in the high uniformity group, accounts for 10% of the intermediate uniformity group and makes up 56% of species with non-uniform germination.

Intermediate germination uniformity is still associated predominantly with a high germination capacity (62%), but intermediate and low capacities are greater than for the highly uniform germinators. Species with low or non-uniform germination (differential dormancy) display a strategy in which low apparent capacity dominates. Such a strategy would appear to depend on spreading the chances of successful germination over time and space. To some extent low germination capacity might reflect limited observations because of time constraints, rather than ultimately low levels of germination.

Samaras

Wind dispersed seeds of all types appear to be generally associated with rapid germination. Augspurger (1984) reported similar results from Barro Colorado Island, where 16 out of 18 wind dispersed seeds had high and rapid germination.

The rapid germination of these species suggests that the timing of maturation and dispersal would be important to ensure the availability of moisture for germination. All samaras were collected between late November and early January, which coincides with the expected start of the wet season.

An extreme example of rapid germination is viviparity, where germination takes place whilst the diaspore is still on the parent tree. This is a characteristic commonly observed in mangroves, and has been recorded in rainforest species in other parts of the world (reported in Vasquez Yanes and Orozco Segovia (1984) from foreign

language publications. It is interpreted as being a mechanism for escaping predation, and also of survival in an uncertain environment (Vasquez Yanes and Orozco Segovia 1984). A.K. Irvine reports viviparity in the wind dispersed samaras of *Argyrodendron* species and *Franciscodendron laurifolium* (both Family Sterculiaceae) in very wet seasons on the Atherton Tablelands (A.K. Irvine personal communication).

It is possible that the viviparity observed in *Blepharocarya involucrigera* in this study may be associated with a lack of wind or excessive moisture impeding dispersal at the time of seed collection (A.K.Irvine personal communication). Germinated seeds have the advantage of rapid establishment when dispersal occurs but may also be prone to dessication if conditions are not favourable.

Dormancy

Slower germination is associated with dormancy. Although there is no clear answer as to where the boundary lies between seeds that are slow to germinate and seeds that are dormant, Baskin and Baskin (1998) proposed the presence of dormancy in tropical rainforest species that take more than four weeks to germinate. The choice of time was based on the fact that high temperatures (typical of the rainforest environment) promote dormancy loss in other communities in seeds with nondeep physiological dormancy after four weeks. Nondeep physiological dormancy occurs when emergence of the radicle is prevented by a physiological inhibiting mechanism of the embryo (Baskin and Baskin 1998). The precise nature of this mechanism is variable, but for many species is likely the result of interaction between the embryo and its covering structures (Baskin and Baskin 1998).

Garwood (1983) reported that over half the 157 woody dicot species surveyed in the seasonal forest of Barro Colorado had germination delayed for more than four weeks, a finding in accord with the observations of Vasquez-Yanes and Orozco-Segovia (1984) on delayed germination in seasonal forests. Just over half the species in this investigation of species from the seasonal rainforests around Cairns also took longer than four weeks to initiate germination.

The study undertaken for this project does not allow for identification of types of dormancy that may exist in individual species, although differential dormancy is identified in species with non-uniform germination curves (see Figure 2.4). Differential dormancy spreads germination in time and potentially in space through increased opportunity for dispersal. This represents an alternative and contrasting germination strategy to that displayed by the highly uniform germinators, and, in a time limited survey of germination, responses would often be associated with low germination capacity. This group is under represented in this study because very slow or low capacity germinators could not be assessed within the 12 week period of observation.

Factors determining the timing of germination

The timing of germination is determined by factors related (a) to the seed and (b) to its environment. Characteristics of the structures covering the embryo (mechanical or chemical impediments) and immature embryos are common seed related factors responsible for delayed germination, while light, moisture, temperature and aeration are important environmental constraints to germination. Parrotta (1995) proposed that biotic factors (*eg* the development of fungal and bacterial populations) appeared to be primarily responsible for the delay in germination on a degraded tropical site in Puerto Rico. The importance of all these factors for germination is known to change over time (Bewley and Black 1994).

Seed-Related Factors and Time to Germination

Baskin and Baskin (1998) define organic dormancy as dormancy caused by some property of the seed or diaspore. Endogenous organic dormancy occurs when germination is prevented by some characteristic of the embryo, for example immaturity. Exogenous organic dormancy is associated with prevention of germination caused by some characteristic of the structures covering the embryo, for example a seed coat that is impermeable to water. Physiological immaturity of the embryo and impermeability of the seed coat are the most common causes of dormancy (Raven *et al.* 1992).

Embryo immaturity

Although causes of dormancy were not specifically studied, some inferences can be drawn from known and recorded germination responses. Family Arecaceae (palms) have underdeveloped embryos and may take a long time to initiate germination (Baskin and Baskin, 1998). In this study, only *Calamus australis* (4 weeks) initiated germination within six weeks. (This seems an unusually short time since in an earlier study, this species took almost twice as long to initiate germination. Possibly the first stage of germination occurred during the weeks that this species remained in the cool room.) *Archontophoenix alexandrae, Ptychosperma elegans* and *Ptychosperma macarthurii* were all intermediate germinators taking 11, 12 and 9 weeks respectively for the start of germination. *Arenga australasica, Linospadix minor* and *Wodyetia bifurcata* did not germinate in white light until after 12 weeks, and *Licuala ramsayi* had not germinated by the conclusion of the study.

Whilst *Wodyetia bifurcata* did not commence germination until after 12 weeks at Atherton, some seeds from the same seed lot were sown in Cairns, and germinated within 12 weeks, suggesting germination could be temperature dependent.

Table 2.1 shows long term mean maximum and minimun temperatures for Cairns, Atherton and Cooktown. Both maximum and especially minimum monthly temperatures are seen to be lower for Atherton than either Cairns or Cooktown.

Table 2.7 Mean monthly maximum and minimum temperatures for Cairns, Atherton and Cooktown

Temperatures are in degrees C

	Cairns		Atherton		Cooktown	
	16.89S	145.76E	17.27S	145.48E	15.45S	145.19E
	Max	Min.	Max	Min	Max	Min
Jan	31.5	23.6	29.0	18.3	32.2	24.2
Feb	31.1	23.7	28.1	18.6	31.7	23.7
Mar	30.5	23.0	27.2	17.8	30.7	23.4
Apr	29.2	21.5	25.6	15.5	29.7	22.4
May	27.5	19.9	23.4	13.5	28.0	21.0
Jun	25.8	17.6	22.1	11.0	26.6	18.4
Jul	25.6	17.0	21.8	10.4	26.4	18.1
Aug	26.5	17.5	22.9	9.9	27.1	18.6
Sep	27.8	18.6	24.6	11.6	28.8	20.0
Oct	29.4	20.5	27.7	13.6	30.2	22.1
Nov	30.6	22.2	29.3	16.0	31.7	23.3
Dec	31.4	23.3	29.7	17.2	32.3	23.9

Source BOM Website

Other families in this study, known to have some species with underdeveloped embryos are Araliaceae, Dilleniaceae, Eupomatiaceae, Myristicaceae, Oleaceae, Piperaceae, Pittosporaceae and Winteraceae (Baskin and Baskin 1998). Further studies are needed to determine if the delayed germination of *Mackinlaya macrosciadea* (Araliaceae), *Hibbertia scandens* (Dilleniaceae) and *Bubbia semicarpoides* (Winteraceae) can be attributed to undeveloped embryos. Early germination was recorded for other representatives of families mentioned above, suggesting that immaturity of embryos was not indicated for these species. *Eupomatia laurina* (Eupomatiaceae), *Piper* spp. (Piperaceae) and *Chionanthus ramiflorus, Jasminum didymum* and *Ligustrum lucidum* (Oleaceae) all showed no delay in germination in this study. In the Family Pittosporaceae there were both intermediate (*Pittosporum wingii*) and late germinators (*Pittosporum venulosum*), as well as *Pittosporum* sp. (=RFK/2369) which did not germinate. A separate study would be needed to explore whether immature embryos were the cause of delayed germination in these species.

Hard seed coats

Hard or fibrous seed coats are associated with the majority of the species with delayed or late germination in white light. Indeed, in the warm and humid environment of the tropical rainforest, a hard seed coat is seen to be a beneficial adaptation to provide protection until endogenous organic dormancy or environmentally imposed dormancy is overcome.

The hard seed coats and related dormancy of species such as *Cassine melanocarpa,* ungerminated by project end, and *Prumnopitys amara,* a late germinator, are cause for speculation. Given tropical rainforest conditions, the period of dormancy seems to extend beyond what would be expected if light and/or temperature requirements had to be met. Possibly these requirements coexist with immature embryos, and sequential satisfaction may be required. Chemical inhibitors in seed coats would be leached out relatively early in the experimental conditions, although inhibitors internal to the seed coat could still exist. Further study might reveal an explanation for this behaviour; on the basis of present knowledge, there is no apparent advantage in a hard seed coat postponing germination for purely mechanical reasons.

Environmental Factors and Time to Germination

Light

This chapter reports on germination in white light only, so no comparison is made here between germination in different light qualities. It will be seen in the following chapter that light quality does affect germination, and that some species germinate in a shorter time in light other than white light.

Temperature

Temperature is known to affect germination, and to interact with other environmental factors, especially light. The postulated effect of temperature in the germination of *Wodyetia bifurcata* has been mentioned above. Although the role of temperature was not the primary focus of this study, it was observed that in the cooler months, the

freshly collected seeds of a number of species failed to germinate. Such a response was seen in both upland and lowland species and those occurring in a wide elevational range and included *Zanthoxylum ovalifolium, Colubrina asiatica, Flagellaria indica* and *Trichosanthes pentaphylla.* Further studies are required to explore the role of temperature in the germination of these species.

Successional status

The successional status attributed to a species is variable, depending on the type of forest in which the species is observed. As a general rule, non-pioneer species are more likely to germinate promptly after dispersal while pioneer species have some sort of dormancy mechanism responsible for delaying germination if conditions are not favourable. However, in this study, unlimited light and moisture might disguise the possibility of delayed germination in the field due to an unsatisfied demand for these prerequisites.

The early germinating species in this study include a number of species that are pioneers, at least in some situations. These are listed below.

Agathis robusta
Blepharocarya involucrigera
Castanospermum australe
Casuarina equisetifolia
Chionanthus ramiflorus
Cryptocarya triplinervis
Ficus adenosperma
Ganophyllum falcatum
Terminalia sericocarpa

At the same time, germination of non-pioneer species with a preference for germination in other light environments might be delayed. Under the conditions of this study, the relationship between successional status and time to germination is not obvious.

Family Menispermaceae

Family Menispermaceae was represented by three species, *Hypserpa laurina, Legnephora moorei* and *Sarcopetalum harveyanum.* All were hard coated late germinators, the seeds of which split longitudinally at germination. Further study is required to determine the cause of late germination, but immaturity of the embryo is a possible cause, along with seed coats that are impermeable to water (A.K. Irvine personal communication). Failure to germinate promptly in white light suggests these species are not light demanding. Temperature does not seem to be a factor, since seeds failed to germinate even in the warmer months. Although this is largely a tropical Family (Jones and Gray 1977), the natural occurrence of *Sarcopetalum harveyanum* over a wide temperature range from New Guinea to Eastern Victoria (van Raders 1999) tends to confirm the irrelevance of temperature as a factor affecting germination in this species. All three species of Menispermaceae had very low levels of germination, leading to speculation that for canopy vines such as these the possibility of almost unlimited expansion in space by vegetative growth might render new growth from seed of secondary importance.

Family Myrtaceae

Early germination was a feature of most Myrtaceae in this study. *Acmena hemilampra, Archirhodomyrtus beckleri, Syncarpia glomulifera, Syzygium angophoroides, Syzygium cormiflorum, Syzygium luehmannii* and *Syzygium tierneyanum* all commenced germination within six weeks. Only *Syzygium kuranda*, which has a less fleshy and more granular pericarp than the other species of *Syzygium* studied, displayed delayed germination, taking 11 weeks to initiate germination. *Acmena graveolens,* characterised by a leathery to woody pericarp (Hyland and Whiffin 1993) did not germinate in the time period covered by this study.

FamilyVerbenaceae

The Family Verbenaceae was represented by five species, none of which were early germinators. *Lantana camara* was collected twice; one sample germinated at eight weeks and the other failed to germinate over the course of this study. This demonstrates the germination variability seen in the same species from different provenances. *Vitex helogiton* had delayed germination (seven weeks), and *Callicarpa pedunculata* germinated after 12 weeks. *Gmelina fasciculiflora* was also collected twice, and had both delayed and late germination. Examination of the seeds of this family suggests hard seed coats might be the cause of slower germination. *Clerodendron tracyanum* did not germinate in white light until more than 20 weeks after sowing. Delayed germination appeared to be a characteristic of this Family group, all of which had hard seed coats.

The families Lauraceae and Sapindaceae were also represented by a number of species, but displayed no obvious defining responses to germination in white light.

A knowledge of germination behavioural traits, especially those seen to have application to family groups, is a potentially useful tool for nursery or rehabilitation programmes based on seed germination. It also promtes greater understanding of natural regeneration processes. Further studies, to include more species and responses over more than one season, would be beneficial to confirm and expand the existing knowledge base.

Conclusion

This investigation of germination and time demonstrated that germination can be categorised as rapid, intermediate or slow depending on the time to initiation of germination. Within these groups there are further divisions based on the uniformity (synchrony) of germination, and the level or capacity of germination achieved. The most common strategy was rapid germination accompanied by high uniformity and high capacity. The least common strategy involved non-uniform germination, with a high proportion of this group having low germination capacity. Between these two extremes was a group with intermediate uniformity, mainly high capacity, but also

intermediate and low capacity of germination. The success of each strategy can only be assessed by its frequency of occurrence, shown here to decline with speed, uniformity and possibly capacity of germination.

There are obvious advantages to using seeds of species that germinate to a high level quickly. Nursery space is conserved with a rapid turnover of seeds/seedlings, and in direct seeding, there is maximisation of results for effort expended in planting and maintenance of revegetation material. The results reported here suggest that for biodiversity maximization, a longer process will be required so that slower germinating species, and those with lower germination capacity are included.

CHAPTER THREE
GERMINATION AND LIGHT QUALITY

3.1 Introduction

The light environment of the tropical rainforest strongly influences plant behaviour and growth form (Chazdon and Fetcher 1984, Mulkey *et al.* 1996, Zagt and Werger 1998). It is not surprising, therefore, that light also appears to be an important factor related to regulating germination of seeds of many tropical rainforest species (Whitmore 1983).

Knowledge of the way in which seeds of tropical rainforest species respond to the light environment, in particular the spectral quality of light, promotes an understanding of the natural recruitment processes in the forest. This knowledge can then be used to facilitate germination both in the nursery and in the field for revegetation and rehabilitation purposes. It also complements the concept of niche differentiation and maintenance of biodiversity *sensu* Grubb (1977).

Seeds respond to the light environment *via* the phytochrome system that has been described in Chapter One. A negative light effect is observed as either a reduction or inhibition of germination, or as delayed germination. The light environment as it relates to germination is described in terms of the ratio of red to far red light (R:FR), defined as the ratio in photon flux density (PFD) at 660 and 730 nm, which are the absorption peaks of the red and far red absorbing forms of phytochrome respectively (Pons 1992).

The relationship between germination behaviour and the light environment is the basis on which rainforest species are divided into two broad ecological groups (Swaine and Whitmore 1988). The most specialised group comprises the pioneer species which germinate only in light with a high R:FR ratio, as is found in sunlight on forest edges, in gaps or in open areas. The balance is made up of non-pioneer or climax species, often also called "shade tolerants", which are reportedly capable of germinating in the leaf canopy shade of the established forest, and often also in sunlight. Within each group there is continuous variation, and for seed germination this varies along a gradient defined by the light environment (Swaine and Whitmore 1988).

Early reports of light, phytochrome and plant responses were based on studies conducted with temperate species (Toole 1973, Frankland 1981, Smith 1981). Studies of tropical rainforest species have largely been confined to comparisons between small numbers of species and germination responses in sun and shade (Vazquez-Yanes 1980, Vazquez-Yanes and Orozco-Segovia 1982, Metcalfe 1996).

There has not yet been a report published on the germination response to light quality of a large number of tropical rainforest species under different light environments. This chapter presents the results of an investigation into the germination responses of 87 species exposed to light of different spectral quality or wavelength.

3.1 Materials and Methods

Collection strategy

Seeds were collected, processed and germinated as described in Chapter Two.
In this investigation into the role of light quality in seed germination, four light treatments were used – white, red, green and black light (or darkness). Clear filter material (Rosco filter) that did not alter the spectral quality of daylight was used for the white light environment. An additional layer of neutral shadecloth (Sarlon 70%) was added to the white light canopy to reduce total transmission. The level of transmission in this treatment was not measured. For red light, Rosco #26 Light Red polyester lighting filter material was used (transmission 12%), and green light was achieved with Lee Filter #129 Primary Green (transmission 15%). Darkness was imposed by using two layers of thick black plastic. All light canopy materials were mounted on metal frames erected on top of seed tables. The transmission spectra for the red and green filters are shown in Figure 3.1. Transmission was measured using an Ocean Optics S2000 spectrometer with Lastrek Spectra-Array 32 software (V 2.11).

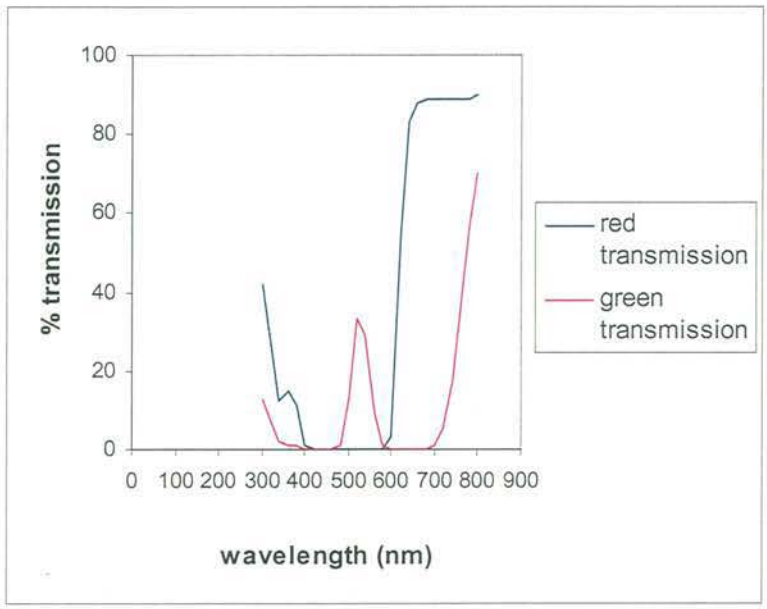


Figure 3.1 Transmission of light through red and green filters

A high level of light transmission through the red filter is evident from around 600 nm. By comparison, the green filter absorbs light between 600 and 700 nm and also between 300 and 500 nm. The latter filter transmission closely resembles light transmission through a leaf canopy, with a R:FR ratio of 0.2 (Metcalfe 1996). Red light has no ecological equivalent, but was included to confirm the effect of light with a high R:FR ratio (*ie* a phytochrome response) in species with a germination response to white light (Vazquez-Yanes and Orozco-Segovia 1982, Bewley and Black 1994). Neutral shadecloth (Sarlon 70%) was used to cover each shadehouse.

Germination conditions

Four replicates of 10 seeds were germinated in each light environment, two replicates randomly placed in each light in each of the two shadehouses (a total of 160 seeds per species). Monthly minimum and maximum temperatures were recorded within each light filter canopy. These descriptive data are represented graphically in Figure 3.2.

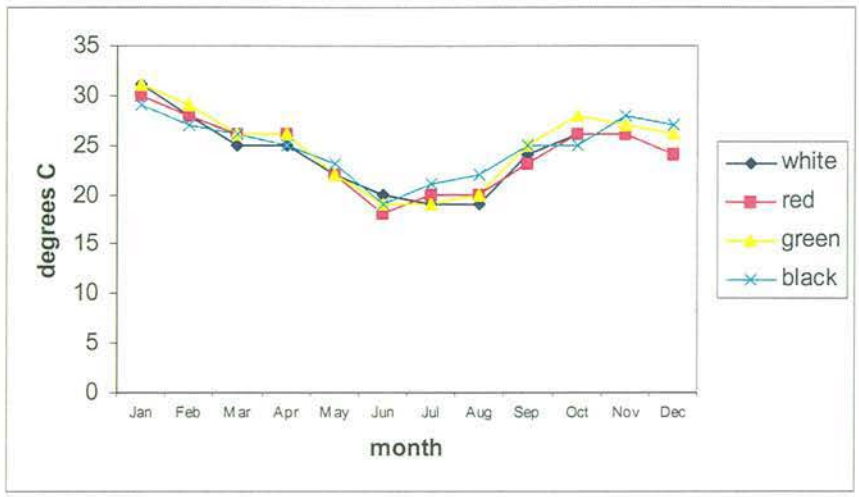


Figure 3.2 Mean monthly temperature in each colour canopy over 12 months

Germination assessments and data analysis

Germination (defined as the visible emergence of the radicle from the seed coat) was recorded weekly where possible for the first 12 weeks after sowing. After this time, most species were removed from the light treatments to make space for new recruits, but some remained and their germination was recorded over later weeks.

A conceptual model in the form of a ternary graph or plot is proposed to better visualise the results of germination in the three ecologically relevant light treatments (Figure 3.3a and b). Ternary graphs plot data on an XYZ coordinate system in the form of three variables that add up to 100% or 1. These variables are typically the normalized proportions of three factors and are plotted on three axes generally arranged as an equilateral triangle. These graphs are also commonly referred to as triangle plots. Percentage germination in each light is shown along the three axes, with 100% germination in a particular light at each apex (e.g. see Figure3.3a). Opposite each apex is an area representing a low percentage of total germination in that light.

Figure 3.3 shows the areas defined to indicate "facilitation" and "inhibition" for each light quality. In the ternary plot 60% or more of total germination in a light treatment is

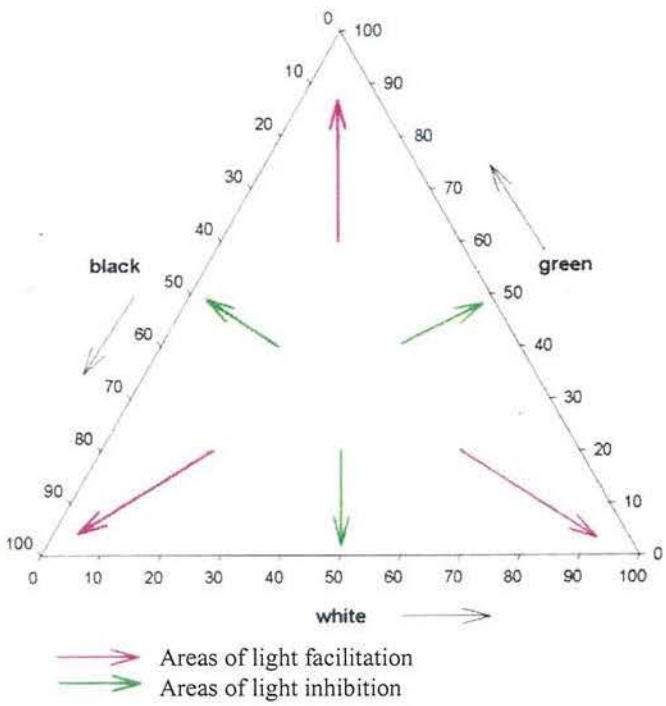
considered to indicate facilitation in that light, while 20% or less is regarded as inhibition in that light.

Kruskal-Wallis tests (df=2) indicate the species with statistically significant germination responses in the three ecologically relevant light treatments. Results for all species are plotted on the ternary plot and species groups, are identified according to the area in which they occur.

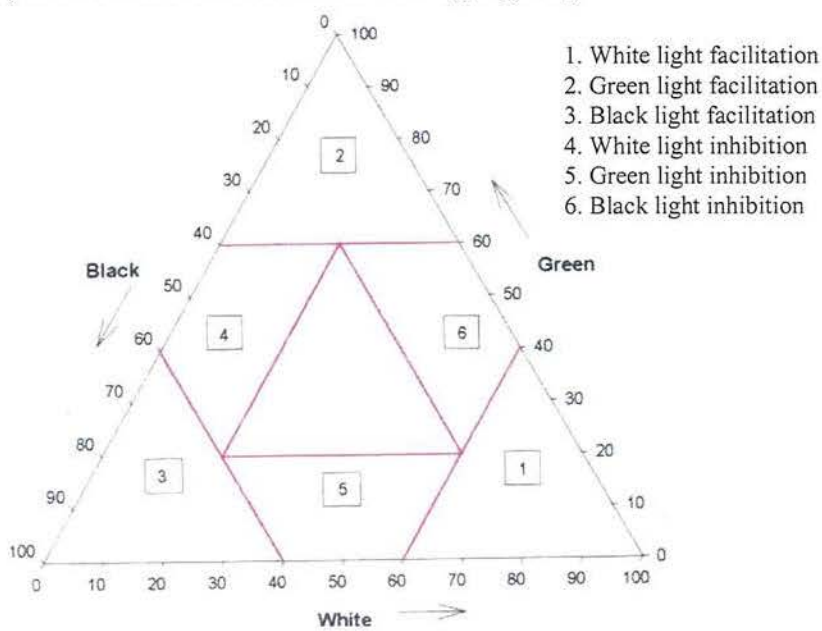
For species with maximum germination in light with a high R:FR ratio, Kruskal-Wallis tests (df=3) are applied to the germination responses in all four light treatments (see Table 3.1).

Figure 3.3: Ternary plots illustrating a conceptual framework for germination responses to three light treatments

(a) Conceptual framework of light facilitation and inhibition



(b) Facilitation and inhibition for each light quality



3.3 Results

Species collected

One hundred and thirty six seedlots comprising 130 species were collected over the course of this investigation. These are listed in Chapter Two. Species that did not achieve a mean maximum germination of 2.5 in at least one light treatment were disregarded. Results for the remaining 87 species are shown in Table 3.1.

Mean maximum germination out of 10 seeds in each light treatment is presented along with standard deviation and Kruskal-Wallis test results. Germination values for each of the three ecologically significant light treatments are plotted in the conceptual framework of the ternary graph in Figure 3.4.

As stated previously, red light was included to confirm the effect on germination of light with a high R:FR ratio. For this reason four light treatments were included in the Kruskal-Wallis test (df=3) for species with mean maximum germination in light with a high R:FR ratio. For all other species, germination results in red light are disregarded for the Kruskal-Wallis test (df=2).

Species with a significant response to light are grouped according to the relative percentages of germination in each light treatment as defined earlier in this chapter. Groups are numbered to correspond to the areas of the ternary plot in which germination responses are located. Thirty seven species showed a statistically significant germination response to the light treatments.

Group 1 contains 12 species with maximum germination in light with a high R:FR ratio. Four sub groups exist within this group – three species that germinated only in light with a high R:FR ratio; five species with zero germination in green light; two with less than 20% germination in green light ; two species with zero germination in darkness. With the exception of one species, *Vitex helogiton*, this a robust group with the results having a strong statistical significance (p=0.012 or less). *Vitex helogiton* is the only questionable member of this group based on its ecology. Despite the effect of light

quality on germination being statistically significant (p=0.047) for this species, the germination rates were relatively low and quite variable. If data from the red light treatment are excluded from the analysis, there is no significant light effect for this species.

Group 2 is unrepresented – there are no species with maximum germination in green light.

Group 3 contains three species with maximum germination in darkness, one of which has zero germination in green light.

Group 4 contains four species with minimum germination in white light.

Group 5 has 13 species, eight with minimum germination in green light and five with zero germination in green light.

Group 6 contains six species with minimum germination in darkness.

Group 7 is the largest group with 50 species for which germination was not significantly affected by light treatment.

Germination results are presented in Figure 3.4.

Table 3.1 Mean maximum germination and standard deviation in each light treatment.
Germination values are the mean number of seeds out of 10 germinating in each of four replicates.
Mean germination values are for week 12 unless otherwise indicated in the column headed Week
Kruskal Wallis H and p values are shown in final columns.

Species name	White	Red	Green	Black	Week	df	H	p
Group 1(a) Species with a requirement for light with a high R:FR ratio								
Alpinia arctiflora	10.00±0.00	9.25±0.26	0.00±0.00	0.00±0.00		3	14.118	0.003
Alpinia caerulea	9.00±1.41	8.00±2.38	0.00±0.00	0.00±0.00		3	13.131	0.004
Pittosporum wingii	3.00±1.15	0.75±0.50	0.00±0.00	0.00±0.00		3	13.321	0.004
Group 1 (b) Species with maximum germination in light with a high R:FR ratio								
Zero germination in green light								
Archirhodomyrtus beckleri	9.00±1.15	10.00±0.00	0.00±0.00	1.50±1.73	18	3	13.421	0.004
Diplocyclos palmatus	5.75±2.06	2.25±2.06	0.00±0.00	0.50±0.58	21	3	10.918	0.012
Pittosporum venulosum	9.00±1.41	7.00±2.16	0.00±0.00	2.50±1.00	25	3	13.597	0.004
Rhodomyrtus pervagata	6.00±0.82	4.50±1.71	0.00±0.00	1.50±1.73	24	3	13.478	0.004
Solanum seaforthianum	9.25±0.96	9.75±0.50	0.00±0.00	5.00±1.63		3	12.742	0.005
Less than 20% germination in green light								
Casearia sp.	7.75±3.30	1.00±1.41	0.50±0.58	1.25±0.96	17	3	9.175	0.027
Vitex helogiton	3.75±1.89	4.25±1.71	0.75±0.96	1.75±1.26	24	3	7.932	0.047
Zero germination in black light								
Ficus adenosperma	5.25±0.50	6.25±0.96	3.00±2.45	0.00±0.00		3	11.846	0.034
Callicarpa pedunculata	6.75±2.36	2.75±3.20	1.75±2.36	0.00±0.00		3	8.658	0.008
Group 2 Species with maximum germination in green light								
Zero species								
Group 3 Species with maximum germination in black light								
Prunus turneriana	5.50±1.29	5.25±2.22	3.75±1.50	8.00±1.41	15	2	5.851	0.054
Tetrastigma nitens	2.75±1.50	5.75±2.63	0.25±0.50	4.75±0.96	31	2	8.889	0.012
Zero germination in green light								
Bubbia semicarpoides	3.00±1.63	1.50±3.00	0.00±0.00	5.75±0.96		2	9.782	0.008
Group 4 Species with minimum germination in white light								
Chionanthus ramiflorus	4.24±2.87	8.50±0.58	7.50±0.58	8.00±1.41	14	2	6.217	0.045
Gomphandra australiana	1.00±1.41	1.25±1.26	3.00±1.41	5.00±2.45		2	7.805	0.050
Ligustrum lucidum	4.75±2.06	5.75±2.50	9.75±0.50	9.00±1.41		2	7.853	0.020
Neolitsea dealbata	3.75±1.71	6.00±0.00	7.75±1.89	9.00±1.41	24	2	7.399	0.025
Group 5 Species with minimum germination in green light								
Antirhea tenuiflora	10.00±0.00	8.75±1.89	4.25±3.20	9.25±1.50		2	8.518	0.014
Ardisia crispa	10.00±0.00	10.00±0.00	1.75±1.50	10.00±0.00	15	2	10.507	0.005
Canarium vitiense	8.00±0.82	8.25±1.71	0.25±0.50	7.25±1.50		2	7.901	0.019
Cupaniopsis anacardioides	9.75±0.50	9.25±0.96	7.25±1.71	9.50±0.58		2	6.933	0.030
Jasminum didymum	9.50±0.58	8.00±0.82	7.50±1.29	9.50±0.58		2	6.316	0.043
Mackinlaya macrosciadea	3.75±0.96	3.00±1.41	0.75±0.50	5.75±3.30	25	2	7.788	0.020
Pararchidendron pruinosum	9.25±0.50	9.00±0.85	7.25±0.96	9.50±0.58		2	8.261	0.016
Scaevola taccada	8.25±0.50	6.75±0.96	7.00±0.82	8.75±0.96		2	6.372	0.041
Zero germination in green light								
Gardenia ovularis	10.00±0.00	10.00±0.00	0.00±0.00	8.75±0.96		2	9.835	0.007
Lasianthus strigosus	4.50±1.29	3.75±4.35	0.00±0.00	6.00±2.00	26	2	7.909	0.019

Species name	White	Red	Green	Black	Week	df	H	p
Parsonsia latifolia	4.00±1.00	1.33±0.58	0.00±0.00	3.00±1.00		2	6.269	0.025
Piper macropiper	10.00±0.00	10.00±0.00	0.00±0.00	8.00±2.71		2	9.835	0.007
Terminalia sericocarpa 1	6.79±1.71	4.50±1.29	0.00±0.00	5.00±2.00		2	8.776	0.012
Group 6 Species with minimum germination in black light								
Archontophoenix alexandrae	8.50±0.58	7.75±2.63	8.00±0.82	5.00±1.83	13	2	7.931	0.019
Blepharocarya involucrigera	9.75±0.50	10.00±0.00	8.75±0.96	7.75±0.96		2	6.190	0.045
Cryptocarya triplinervis	8.00±1.41	8.50±0.58	8.50±0.58	4.25±1.50		2	7.922	0.019
Synima cordierorum	2.75±0.96	3.50±1.73	4.75±3.10	1.00±0.58		2	6.895	0.032
Tetrastigma thorsborneorum	5.75±0.96	5.50±0.58	4.50±1.00	2.50±1.00		2	7.928	0.019
Group 7 Species with no light effect on germination								
Acmena hemilampra	3.50±2.08	4.50±1.91	3.75±2.63	6.75±1.71	14	2	3.286	0.193
Agathis robusta	7.25±2.22	7.00±2.00	5.50±1.91	7.00±1.83		2	1.459	0.482
Aglaia sapindina	8.75±0.50	8.25±0.50	8.25±1.71	8.00±1.15		2	0.707	0.702
Argyrodendron polyandrum 1	9.25±0.96	9.25±0.96	9.25±0.96	9.25±1.50		2	0.015	0.930
Argyrodendron polyandrum 2	8.25±0.50	8.75±0.96	7.50±1.00	9.00±1.41		2	3.192	0.200
Calamus australis	9.75±0.50	9.75±0.50	10.00±0.00	10.00±0.00		2	2.000	0.368
Cardwellia sublimis	10.00±0.00	9.75±0.50	10.00±0.00	9.75±0.50		2	2.000	0.368
Carnarvonia araliifolia	9.75±0.50	10.00±0.00	9.75±0.50	9.50±1.00		2	0.050	0.975
Castanospermum australe	9.75±0.50	8.25±0.96	9.75±0.50	9.50±1.00		2	1.019	0.601
Castanospora alphandii	5.50±2.38	5.25±1.50	5.00±2.16	5.00±1.41		2	0.129	0.938
Casuarina equisetifolia	7.00±1.41	5.50±3.41	7.75±2.06	6.75±1.89		2	0.373	0.830
Centrosema pubescens	10.00±0.00	8.75±1.26	8.75±0.96	9.00±0.82		2	4.991	0.082
Cerbera floribunda	8.50±1.29	9.00±1.15	9.00±0.82	10.00±0.00	18	2	5.008	0.114
Clerodendron tracyanum	4.75±0.96	3.00±3.56	2.75±3.50	2.00±2.45	29	2	2.967	0.252
Cordyline cannifolia	5.25±2.36	8.00±1.41	6.75±2.21	8.50±1.73	14	2	5.437	0.066
Corynocarpus cribbianus	9.50±0.58	9.75±0.50	9.75±0.50	10.00±0.00		2	2.444	0.295
Cryptocarya hypospodia 1	5.75±2.06	6.25±1.71	6.25±2.87	8.00±2.71		2	3.104	0.212
Cryptocarya hypospodia 2	1.25±1.89	1.25±1.29	1.25±1.89	5.50±3.70		2	3.125	0.210
Cryptocarya murrayi	2.25±3.00	4.75±3.86	6.25±3.30	6.25±0.50		2	5.068	0.079
Darlingia darlingiana	9.75±0.96	9.00±0.82	9.50±0.58	9.50±1.00		2	0.596	0.724
Elaeagnus triflora	9.25±0.96	9.75±0.50	8.50±0.58	9.25±0.50		2	2.750	0.253
Endiandra insignis	9.00±0.00	10.00±0.00	9.00±0.00	9.50±0.71		2	2.000	0.368
Eupomatia laurina	5.00±3.83	7.75±1.26	7.75±0.50	7.75±2.22		2	1.567	0.457
Evodiella muelleri	2.25±2.63	3.50±1.00	2.50±2.38	0.00±0.00		2	4.752	0.093
Flindersia ifflaiana	9.00±0.82	8.25±0.96	9.50±0.58	8.25±0.50		2	5.118	0.077
Ganophyllum falcatum	9.25±0.96	8.75±0.96	8.50±1.92	8.67±1.15		2	0.522	0.770
Glycosmis trifoliata	10.00±0.00	10.00±0.00	9.50±0.58	9.75±0.50		2	2.444	0.295
Hibbertia scandens	0.75±0.96	3.50±4.73	0.00±0.00	1.75±2.36	25	2	2.750	0.253
Hodgkinsonia frutescens	8.00±2.16	5.75±1.71	7.00±4.76	8.25±0.50	14	2	0.396	0.820
Ipomoea hederifolia	7.75±0.96	6.75±0.50	8.00±0.82	7.25±0.96		2	1.197	0.550
Micromelum minutum	8.00±1.83	8.25±0.96	7.50±1.29	6.75±2.06		2	0.649	0.732
Mischocarpus exangulatus	10.00±0.00	10.00±0.00	10.00±0.00	10.00±0.00		2	0.000	1.000
Piper caninum	10.00±0.00	9.75±0.50	9.25±0.96	9.75±0.50		2	2.617	0.270
Piper novae-hollandiae	9.25±0.96	9.75±0.50	10.00±0.00	10.00±0.00		2	4.364	0.113
Podocarpus grayae	7.25±2.06	6.25±3.10	6.25±1.26	6.75±2.22		2	0.652	0.722
Pouteria obovoidea	8.25±0.50	9.25±0.50	8.75±1.50	9.00±0.00		2	2.038	0.361
Ptychosperma elegans	3.75±1.44	1.75±0.63	1.50±0.87	4.00±1.29	13	2	2.198	0.333
Randia sessilis	9.50±1.00	7.25±2.22	7.00±2.16	8.75±0.96		2	2.500	0.287
Rivina humilis	9.25±0.50	10.00±0.00	8.50±1.91	8.75±0.96		2	0.546	0.761
Salacia chinensis	8.50±1.00	8.25±1.71	7.00±0.89	9.25±0.96	18	2	5.450	0.066
Syncarpia glomulifera	5.25±3.59	1.50±3.00	0.75±1.50	1.25±1.50		2	3.672	0.158
Syzygium angophoroides	9.50±0.58	9.00±1.00	9.50±0.58	9.00±1.41		2	0.143	0.931
Syzygium cormiflorum	10.00±0.00	9.25±0.50	9.75±0.50	10.00±0.00		2	2.000	0.358
Syzygium kuranda	5.25±2.06	5.75±1.50	3.75±0.96	7.00±1.63	17	2	2.435	0.296
Syzygium luehmannii	7.25±2.06	9.25±0.96	5.00±3.46	5.00±1.83	13	2	3.241	0.198
Syzygium tierneyanum(red)	10.00±0.00	10.00±0.00	9.50±0.58	10.00±0.00		2	0.000	1.000
Syzygium tierneyanum(white)	10.00±0.00	10.00±0.00	10.00±0.00	10.00±0.00		2	4.400	0.100
Terminalia sericocarpa 2	5.25±2.22	5.75±2.50	6.00±1.41	5.25±1.26		2	0.608	0.738
Toechima erythrocarpum	9.25±0.50	9.50±1.00	7.25±4.19	8.75±0.96		2	0.749	0.688
Trophis scandens	7.50±1.73	7.75±0.96	9.25±0.50	9.25±0.96		2	4.605	0.100

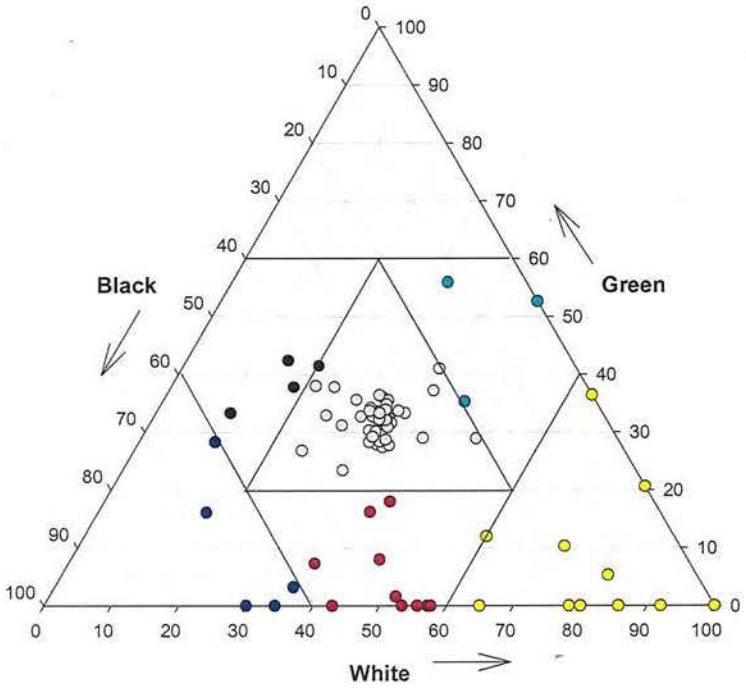


Figure 3.4. Germination responses to light quality for 87 species

Germination response groups

Seeds 'sense' their light environment *via* the phytochrome system that has been described in Chapter One. For species that are sensitive to light quality, a high proportion of germination in white or red light indicates that germination is facilitated in light with a high R:FR ratio. For these species a low R:FR ratio, as found in green light, reduces or delays germination (Pons 1986). This is the classical phytochrome response.

The main light treatments producing obvious germination responses were white light and green light, with high and low R:FR ratios respectively. The number and percentages of species in each light response groups is shown in Table 3.2. These are species with a statistically significant germination response to light.

Table 3.2 Number of species in each group and as a percentage of total seedlots

Response group	Number of species	% of total
1 (maximum germination in light with high R:FR)	12	14
2 (maximum germination in green light)	0	0
3 (maximum germination in darkness)	3	3
4 (minimum germination in white light)	4	5
5 (minimum germination in green light)	13	15
6 (minimum germination in darkness)	5	6
7 (germination not affected by light quality)	50	57

Light response groups and time to germination

Although a Kruskal-Wallis test showed time to germination was not significantly different between the light response groups (H=4.6, p=0.466) some non-statistical observations can be made. Species in the two major ecological groups (Group 1 with a maximum germination in light with a high R:FR ratio and Group 5 with minimum germination in light with a low R:FR ratio) and Group 6 (minimum germination in darkness) were more likely to be rapid germinators (see Table 3.3). Species in Group 3 (maximum germination in darkness) and Group 4 (avoidance of white light) were more frequent germinators after 6 weeks. The demonstration of negatively photoblastic germination responses in the latter groups raises the possibility that other physiological responses, such as time to germination, might also manifest in 'opposite' ways.

Table 3.3 Light response groups and time to germination

	Time to germ												
	number of species in each week												
week	1	2	3	4	5	6	7	8	9	10	11	12	>12
response group													
1(max germ in high R:FR)	1		2	3	1	1	1			1		1	2
3(max germ in B)							1		1	1			
4(min germ in W)				2							1		1
5(min germ in G)		2	4	3	1	1			1		1		
6(min germ in B)	1		1	2	1								
7(no light response)	10	17	4	2	4	4		2		1	2	1	3

B=Darkness, W=white light, G=green light

Group 7, the non-responsive germinators, had a majority of species that were rapid germinators, conforming to the paradigm that non-pioneer seeds of the tropical rainforest generally germinate promptly (Whitmore 1984), which is supported by the results of this study.

3.4 Discussion

To date there has been limited work in the area of germination of seeds of the tropical rainforest as it is affected by light quality. Such studies as have been published tend to consider only sunlight and shade and a small number of species (Vazquez-Yanes 1980; Vazquez-Yanes and Orozco-Segovia 1982 ;Vazquez-Yanes and Smith 1982; Augspurger 1984; Metcalfe 1996). In this study, a large number of rainforest species has been investigated for germination responses to four light treatments (white, red, green and black), three of which are represented ecologically in natural conditions (white, green and black). Red light responses were considered only in support of germination in white light, since both these environments have a high R:FR ratio. In most species, the germination response in red light was similar to that in white light, and different to germination in green and black light.

Although species were classified in seven groups according to their germination responses to light, the most obvious results were a demand for light with a high R:FR ratio, an avoidance of light a low R:FR ratio, and a large group for which germination was not affected by light quality.

It is highly significant that there were no species with a preference for germination in green light (low R:FR ratio). Only two species (2% of 87 species) had more than 50%

of total germination in green light and 25 species (29%) had less than 20% of total germination in green light.

Ecologically, it is important for a seed to be able to 'sense' its light environment because it is an indication of the conditions under which its seedlings will establish and mature. Green light would normally indicate the presence of a canopy above, and light sensitive species in this environment would fail to germinate until or unless a canopy gap was created. Black light or darkness, sends a more ambiguous message, possibly indicating coverage by litter or soil, either of which could be a temporary situation. Most importantly, the absence of light means also the absence of the inhibitory effects of green light. Species with zero germination in black light would be expected to survive in soil seed banks where they might persist until disturbance altered the light regime.

Group 1 species demonstrated a need for light with a high R:FR ratio, and three species germinated exclusively in this light environment. The other species in the group had some germination in other light treatments, though at low levels; two species failed to germinate in black light and a further five failed in green light. A preference for light with a high R:FR ratio coupled with avoidance of light with a low R:FR ratio, is a defining feature of pioneer species of the tropical rainforests (Whitmore 1989) and the current work further supports this interpretation with the distribution of the species in this group confirming their pioneer status.

Alpinia arctiflora, Alpinia caerulea and *Pittosporum wingii* are seen mostly in gaps and on edges, and tend to disappear when marked overshading occurs (A.K. Irvine pers.comm.). The remaining species in this group are also generally found in high light situations of disturbance or on forest margins, where light with a high R:FR ratio would be available for at least part of the day. *Casearia* sp. occurs in a variety of situations; results of this study indicating maximum germination in white light suggest dispersal could be important for this species.

Group 3 responses indicate that the three species in this group germinate best in darkness. *Bubbia semecarpoides* is an understorey tree in well developed rainforests (Hyland and Whiffin 1993) where low light situations would be abundant, but it is

interesting that germination was absent in green light. It is possible dark germination has been selected as a defence against desiccation on the soil surface. *Prunus turneriana* and *Tetrastigma nitens* also had low germination in green light. These seeds probably have sufficient Pfr to stimulate germination in darkness, but are responsive to R and FR light as well (Shinomura 1997). The dark germination of this group may simply reflect the absence of the inhibitory effects of a low R:FR ratio as found in green light. The species in this group tended to have late and low germination, and should be investigated further in studies without time constraints so that ultimate germination can be observed.

Group 4 species are defined as demonstrating avoidance of white light. Like the species in Group 3, these species apparently have sufficient Pfr in the seed for germination in darkness, but are still responsive to the R:FR ratio of light. As an understorey tree in well developed lowland rainforest (Hyland and Whiffin 1993), *Gomphandra australiana* seeds would readily find suitable dark germination sites. *Ligustrum lucidum* and *Neolitsea dealbata* are both associated with disturbance, but the results observed here suggest that germination would be enhanced by burial of the seed (see Panetta 2000, for *L. lucidum*). Seedlings of *Neolitsea dealbata,* a species that can persist in a high light environment or in subcanopy shade (A.K. Irvine pers. comm.) are abundant on the floor of the established forest (pers.obs.) and also in the shade of the parent tree. For the species in this group, black light or darkness would appear to be associated with burial by soil or litter.

Avoidance of green light is the dominant characteristic of the species in Group 5, indicating that at the point of germination, these species behave as 'pioneers', even though as adults many are found within the mature forest.

There is a variety of lifeforms represented in Group 5. Some species are commonly seen on forest edges (*Ardisia crispa* -an exotic-and *Mackinlaya macrosciadea*), while the vines *Parsonsia latifolia* and *Piper macropiper* have seeds readily dispersed to unshaded spots by wind and animal dispersal respectively. Most of the remaining species are found as understorey plants in well developed forests, and would have to rely on dispersal or partial sunlight from gaps to find suitable unshaded germination sites. *Terminalia sericocarpa* is known to be a major food source for frugivorous birds

that disperse the seeds after consuming the flesh. *Gardenia ovularis* requires a high R:FR light environment at the time of germination but becomes shade tolerant as a sapling/adult tree, persisting in the mature forest (A.K. Irvine pers. comm.).

Photoreversible germination response was demonstrated by ungerminated seeds of *Terminalia sericocarpa* that promptly germinated when removed from the green light environment to white light at the end of 12 weeks. Studies of the time taken to reverse the inhibiting effects of FR light would be interesting, as this should give an indication of whether transient light from sunflecks or gaps is adequate for germination, or if longer term exposure is required.

Avoidance of darkness characterises the species of Group 6. These tended to have almost equal germination in white and green light and possibly are not light responsive apart from avoiding darkness. It is not yet known what mechanism controls enhancement or reduction of light-independent dark germination (Shinomura 1997).

Conclusion

The novel presentation of germination responses to light quality in a ternary plot allows visualisation of a species' optimal light environment for germination within the range of possibilities existing under natural conditions. At the same time, this framework illustrates for each species its optimal germination light environment in relation to that of other species, and where a species' germination behaviour lies along the continuum of the spectral quality of light that characterises the light environment of tropical rainforests (Canham 1989).

The data presented in this study will be useful to those raising seed in nurseries for revegetation of forests, or for other commercial ends. Germination yields could be maximised and expedited by placing seeds in appropriate light environments. In direct seeding for revegetation or rehabilitation, germination responses to light indicate that the specific requirements or preferences of some species will dictate where they should be sown for maximum results. In all cases where rainforest seeds are to be germinated, it seems the best results will be achieved by using those species which have been shown

to germinate equally well in any naturally occurring light environment, unless the light preferences of particular species can be provided.

Repeated studies of this nature, both within and between provenances, should be significantly complementary to ecological studies of niche differentiation and maintenance of species diversity *sensu* Grubb (1977).

CHAPTER FOUR

SPECIES ATTRIBUTES AND GERMINATION

4.1 Introduction

Although the main focus of this study was to investigate the role of light quality in germination, it was considered worthwhile to integrate other attributes with the germination findings. In this chapter, a preliminary exploratory approach is taken, using data from the literature in combination with the results described in earlier chapters. So defined, the contents of this chapter are largely speculative in nature, suggesting interesting areas for future studies. Seed size, diaspore type, mode of dispersal and the maternal light environment are considered in relation to possible associations with germination behaviour.

4.2 Materials and Methods

Seed size was investigated as it related to white light germination and also time to initiation of germination for all species studied, and also for intrafamily and intrageneric groups where data were available. Seed dimensions as recorded by Hyland and Whiffin (1993) and Cooper and Cooper (1994) are used. Seed dimensions are given as the length of the longest axis.

Diaspore structure, dispersal and the maternal light environment are also considered in relation to germination behaviour using data from earlier chapters and literature on the subject.

4.3 Results

Seed size and light response

For all species, there is a weak negative correlation between seed size (mean length) and percentage of total germination in white light (Spearman's rho = -0.471, significant at p = 0.01). This relationship is shown in Figure 4.1.

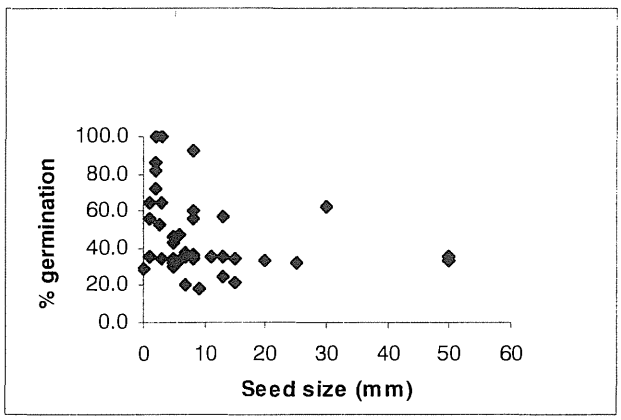


Figure 4.1 Seed size and percentage of total germination in white light.

This trend is also seen in a comparison of mean values for seed size for each light response group, shown in Table 4.1.

Table 4.1 Size ranges and mean size of seeds in germination light response groups.
Number of species for which data is available is shown in brackets

Species light response group	Response profile	Seed size range(mm)*	Mean seed size (mm)*
Group 1	Max. germination in white light	1-8 (10)	3.3
Group 3	Max. germination in darkness	5-30 (5)	13.8
Group 4	Min. germination in white light	7-25 (4)	14.8
Group 5	Min. germination in green light	1-30 (10)	10
Group 6	Min. germination in darkness	6-13 (4)	10.3
Group 7	no light response	1-50 (45)	15

*Source Hyland and Whiffin (1993) and Cooper and Cooper (1994)

Group 1 species, with over 60% of total germination in white light, have a mean seed size markedly smaller than any of the other light response groups. Mean seed size increases as light responses vary from dominance by white light germination, until

maximum size is reached for species with no light preference for germination. It is interesting to note that Groups 3 and 4, which are not associated with high levels of germination in white light, have mean seed size almost the same as the Group 7 species.

Some families were represented by a number of species with different responses to light quality enabling comparisons of seed size and light response to be made within related groups (see Kelly and Purvis 1993). These families and species are shown in Table 4.2.

Table 4.2 Seed size and percentage of total germination in white light

Family	Species	Seed size* mm	% white germination
Arecaceae	*Archontophoenix alexandrae*	15	40
	Calamus australis	10	33
	Ptychosperma elegans	15	41
	Ptychosperma macarthurii	13	30
Lauraceae	*Cryptocarya hypospodia 1*	18	29
	Cryptocarya hypospodia 2	18	16
	Cryptocarya murrayi	18	15
	Cryptocarya triplinervis	13	39
	Endiandra insignis	50	33
	Neolitsea dealbata	9	18
Myrtaceae	*Acmena hemilampra*	13	25
	Archirhodomyrtus beckleri	2	86
	Rhodomyrtus pervagata	2	80
	Syncarpia glomulifera	2	72
	Syzygium angophoroides	9	34
	Syzygium cormiflorum	32	34
	Syzygium kuranda	40	33
	Syzygium luehmannii	5	42
	Syzygium tierneyanum	8	34
Oleaceae	*Chionanthus ramiflorus*	15	22
	Jasminum didymum	8	36
	Ligustrum lucidum	7	20
Piperaceae	*Piper caninum*	3	35
	Piper macropiper	1	56
	Piper novae-hollandiae	5	32
Rubiaceae	*Antirhea tenuiflora*	12	43
	Gardenia ovularis	2.5	56
	Hodgkinsonia frutescens	8	34
	Lasianthus strigosus	5	43
	Randia sessilis	7	37
Rutaceae	*Evodiella muelleri*	6	47
	Flindersia ifflaiana	15	34
	Glycosmis trifoliata	8	34
	Micromelum minutum	7	36
Sapindaceae	*Castanospora alphandii*	30	36
	Cupaniopsis anacardioides	9	37
	Mischocarpus exangulatus	20	33
	Synima cordierorum	11	32
	Toechima erythrocarpum	15	37
Verbenaceae	*Callicarpa pedunculata*	2	79
	Clereodendron tracyanum	5	50
	Vitex helogiton	8	60

*Source Hyland and Whiffin (1993) and Cooper and Cooper (1994)

There are two levels of response to be considered in these results – relationships that are seen at the family level, and those at the genus level. In the negatively photoblastic species (those with maximum germination in darkness and/or slow or low germination in white light) small seed size was associated with lower levels of germination in white light, the reverse of the general trend described before. This is seen in the Arecaceae, Lauraceae and Oleaceae families. Within the Arecaceae family group, comparison of the two *Ptychosperma* species reflects lower germination in white light in the smaller seeded species.

All species in Family Lauraceae initially displayed negatively photoblastic responses, with faster and/or higher germination in darkness. At the *Cryptocarya* genus level in Family Lauraceae, the relationship between seed size and germination in white light was the same as in positively photoblastic species. The smallest-seeded species, *Cryptocarya triplinervis,* had the highest level of germination in white light; it was also the only *Cryptocarya* with maximum germination in white light at the conclusion of observations. When germination is considered at the family level, the pattern of response is reversed, reflecting the negatively photoblastic nature of this group. The largest seeds of *Endiandra insignis* had maximum germination in white light while *Neolitsea dealbata,* with the smallest seed, had the least germination in white light.

Archirhodomyrtus beckleri, Rhodomyrtus pervagata and *Syncarpia glomulifera* with the smallest seeds in the Myrtaceae family group, had maximum germination in white light. At the *Syzygium* genus level, the smallest-seeded *Syzygium luehmannii* is seen to have the highest level of germination in white light.

In the Family Oleaceae germination was significantly affected by light quality for the exotic *Ligustrum lucidum* which had the smallest seed in this family group and a negatively photoblastic response of minimum germination in white light.

The smallest seed of the *Piper* genus, *Piper macropiper,* was associated with the highest level of germination in white light, while for Family Rubiaceae the pattern of small seed/high white light germination is visible if *Antirhea tenuiflora* is excluded.

For Family Rutaceae, one of the smallest seeded-species, *Evodiella muelleri,* had the highest level of germination in white light, but there is not a clear trend in this family. In the Family Sapindaceae germination in white light does not differ greatly between species with varying seed sizes. The smallest seed of *Callicarpa pedunculata* recorded the highest level of white light germination in the Family Verbenaceae, but all species in this family recorded high germination in the white light environment.

Seed size and time to germination

The mean seed size for species germinating in each week is shown in Table 4.3.

Table 4.3 Mean seed size for species germinating in each week

Number of species = number for which size data is available

week of germination	number of species	mean seed size* (mm)
1	11	16.5
2	17	14.4
3	11	9.2
4	13	6.7
5	7	18.0
6	5	6.2
7	3	11.0
8	3	6.7
9	3	9.7
10	4	15.3
11	5	19.0
12	4	7.5

*Source Hyland and Whiffin (1993) and Cooper and Cooper (1994)

There is no obvious overall pattern to seed size as it relates to time of germination, except for the first four weeks, when seed size is seen to decrease over time.

Week of germination and seed size are shown for family groups in Table 4.4.

Table 4.4 Seed size and week of germination for family groups

Family	Species	Seed size* mm	Week of germination
Arecaceae	*Archontophoenix alexandrae*	15	11
	Calamus australis	10	4
	Ptychosperma elegans	15	12
	Ptychosperma macarthurii	13	9
Lauraceae	*Cryptocarya hypospodia 1*	18	3
	Cryptocarya hypospodia 2	18	5
	Cryptocarya murrayi	18	10
	Cryptocarya triplinervis	13	3
	Endiandra insignis	50	2
	Neolitsea dealbata	9	21
Myrtaceae	*Acmena hemilampra*	13	5
	Archirhodomyrtus beckleri	2	4
	Rhodomyrtus pervagata	2	12
	Syncarpia glomulifera	2	1
	Syzygium angophoroides	9	2
	Syzygium cormiflorum	32	1
	Syzygium kuranda	40	11
	Syzygium luehmannii	5	2
	Syzygium tierneyanum	8	1
Oleaceae	*Chionanthus ramiflorus*	15	4
	Jasminum didymum	8	3
	Ligustrum lucidum	7	4
Piperaceae	*Piper caninum*	3	6
	Piper macropiper	1	4
	Piper novae-hollandiae	5	3
Rubiaceae	*Antirhea tenuiflora*	12	2
	Gardenia ovularis	2.5	4
	Hodgkinsonia frutescens	8	6
	Lasianthus strigosus	5	9
	Randia sessilis	7	2
Rutaceae	*Evodiella muelleri*	6	5
	Flindersia ifflaiana	15	1
	Glycosmis trifoliata	8	2
	Micromelum minutum	7	1
Sapindaceae	*Castanospora alphandii*	30	2
	Cupaniopsis anacardioides	9	4
	Mischocarpus exangulatus	20	2
	Synima cordierorum	11	4
	Toechima erythrocarpum	15	4
Verbenaceae	*Callicarpa pedunculata*	2	17
	Clereodendron tracyanum	5	23
	Vitex helogiton	8	7

*Source Hyland and Whiffin (1993) and Cooper and Cooper (1994)

For Families Arecaceae and Sapindaceae, the time to initiation of germination appears to increase as seed size decreases. There are no discernible patterns for any of the other related groups.

Diaspore type

Multiple seeds within the fruiting body characterise the diaspores of Group 1 species (with the exception of *Callicarpa pedunculata*) with maximum germination in light with a high R:FR ratio, and species of Family Rubiaceae, whose light requirement is expressed as avoidance of green light.

Dehiscence of fruits in this study appeared to have no relationship with germination response to light quality. Twenty five percent of the seeds in this study were associated with dehiscent fruits, and 21% of these were responsive to the light environment at germination. For the remaining indehiscent species, 28% were light sensitive. The proportion of light sensitive species was not significantly different between the two groups (Chi square = 0.8 for df=3, not significant at the 0.05 level.)

Seed dispersal

There are no obvious patterns of dispersal in relation to light requirements for germination.

Maternal light environment

Since this was not specifically investigated, the effect of the maternal light environment remains a subject for speculation, and is covered in the Discussion below.

4.4 Discussion

Seed size and light response

In 1942 Salisbury reported that seeds of pioneer species which typically become established in sunlit habitats tend to have smaller seeds than climax species which become established in closed, shaded habitats. Baker (1972) reported similar findings for seed size and habitat in Californian trees. Salisbury postulated that this correlation was most likely associated with the need to support an appropriate level of growth until the seedling could become self-supporting in its natural habitat. Since that time, numerous authors have investigated seed size and sought to clarify its adaptive relevance (*eg* Janzen 1969; Foster and Janson 1985, Foster 1986; Hladik and Miquel 1990; Armstrong and Westoby 1993; Metcalfe 1996; Crawley 1997; Grubb 1998.).

Selection would be expected to favour that seed size which is a compromise between number and size and the ecological niche of each species (Armstrong and Westoby 1993). It follows that small seeded species should be associated with high light environments, whilst large seeds would seem to meet the regeneration and survival requirements of species growing in the forest shade. The light requirement associated with small seeds is believed to be important for sensing the depth to which a seed is buried (Pons 1992), and for preventing germination until suitable light conditions are encountered after disturbance. The hard seed coats associated with many small seeded pioneer species protect the seed during the period of light imposed dormancy.
A broad range of seed sizes is found in the tropical rainforests of north east Queensland, from tiny seeds less than 1 mg (e.g. *Melastoma affine*) to very large seeds such as that of *Idiospermum aulstraliense* (Grubb and Metcalfe 1996), reported to have a fresh weight of as much as 225g (Worboys 1999). In this investigation, seeds ranged in size from the tiny *Piper macropiper* (approximately 1mg) to those of *Endiandra insignis* (> 13g), *Syzygium cormiflorum* (>21g) and the dense seeds of *Castanospermum australe* with a fresh weight of 41g.

In general, within related groups in this study, small seed size seemed to be associated with higher levels of germination in white light, as has been reported in other studies (Foster 1986; Osunkoya 1996). The exceptions are species with negatively photoblastic

germination responses, which tended to show a reverse pattern. Responses for Sapindaceae need to be clarified by germination trials over more than one season.

The greatest variation in seed size was seen to be between the *Piper* species. Mean dry seed mass of the white light demanding *P. macropiper* was 0.0009mg, while for *P. caninum* and *P. novae-hollandiae* values were .026g and 0.027g respectively. Grubb (1998) suggested that a possible explanation for this substantial difference in seed size might be the length of time the species has been present in the tropics, which allowed for diversification in seed mass (at the same time conceding that this had not occurred in Moraceae).

Three out of five species representing Family Rubiaceae demonstrated a light sensitivity in this study. The two apparently non-sensitive species, (*Hodgkinsonia frutescens* and *Randia sessilis)* on closer examination were found to have had some difference in germination levels over time. In both cases, germination was delayed in green light and darkness relative to white light. This suggests that light sensitivity (albeit a temporary phenomenon) might be a characteristic of this family, unrelated to seed size, a view supported by the findings of Metcalfe (1996). In a study of small-seeded tropical rainforest plants exposed to different spectral compositions, Metcalfe found that three species of Family Rubiaceae responded in a broadly similar way to their confamilials (delayed or reduced germination in shade or darkness) that was distinctly different from species in other families. Additional studies are needed to explore this proposition.

The variation in seed size that occurs within a species, and even within a crop, has been noted in earlier studies. Green (1999) reported that seed mass varied more than 30-fold in *Chrysophyllum* sp.nov. (Sapotaceae), and Wulff (1985) found a 10-fold variation in seeds of *Hyptis suaveolens* (Labiateae) from a single population. Wulff noted that the smaller seeds of *Hyptis suaveolens* required light with a higher R:FR ratio for germination than did the larger seeds; and interpreted this as indicating that different sized seeds could be favoured in different forest microclimates. She suggested that this plasticity in seed size might retard selection. This may be so, but plasticity would better serve survival in the uncertain environment of the rainforest with light and moisture varying greatly within the forest and over time, especially in seasonal forests.

In addition to light requirements for germination, other plant characteristics have been shown to be related to seed size. In 11 sympatric species of *Macaranga* in Borneo, maximum tree size, seed size, absolute tree size at the onset of reproduction and annual fecundity were all shown to covary with the degree of shade tolerance (Davies and Ashton 1999). Fruit size, seed size, hardness of seed coat, seedling cotyledon function, fruit maturation period and, to a lesser extent, seed number per fruit and wood density were found to be predictive of light requirement, with and without the effects of phylogeny, for 89 woody plant species from the tropical rainforests of north Queensland (Osunkoya 1996).

For comparisons between taxa, seed size as it relates to light requirements for germination is seen to be a comparative rather than an absolute measure. The smallest of the Lauraceae seeds are larger than the two larger-seeded species of Piperaceae. Such a range of seed sizes in the study species bears out Grubb's (1998) reference to "inappropriate" seed size for regeneration class when comparisons are made at the community level.

Seed size and time to germination

It is an interesting observation that in the first four weeks, mean seed size decreased while the time to germination increased. Bearing in mind Baskin and Baskin's (1998) postulation that seeds which germinate after four weeks have some kind of dormancy, these results might reflect a simple but crude size/time relationship which is lost when time to germination is affected by dormancy mechanisms.

Within family groups of species, there seems to be no consistent relationship between seed size and time to germination, except for Arecaceae and Sapindaceae which are coincidentally the families lacking a relationship between seed size and light response. In these two families, larger seeds germinated before smaller seeds. Further studies are needed to determine the relevance, if any, of this result.

Whist overall patterns within most families are absent, in some cases individual species conform to expected behaviour of larger seeds germinating more rapidly than smaller seeds (Fenner 1985; Foster 1986). In Family Lauraceae, *Neolitsea dealbata* with the

smallest seeds of all Lauraceae species in this study, took the longest time to initiate germination in white light and *Endiandra insignis,* with the largest seed, germinated most rapidly.

Diaspore type

The relationship between multiple seeds per fruit, maximum germination in white light and avoidance of green light has been mentioned above in Results. Both seed number per fruit and seed size have been shown previously to be predictors of the light requirement of species of the rainforests of north east Queensland (Osunkoya 1996). The structure and size of diaspores is related to the manner in which they are dispersed to a germination site.

Seed dispersal

Seed dispersal is the means by which seeds arrive at a site suitable for germination. It also provides the chance of escape from competition with the parent tree and siblings, and potentially from predation (Janzen 1970,1972,1975). Additionally, dispersal influences the genetic composition of plant communities by the introduction of new individuals and genotyes (Howe 1989, Brewer and Rejmanek 1999).

Modes of dispersal of plant species are presumably the result of natural selection for features that favour arrival at sites suitable for germination (Fenner 1985). Where a light requirement exists for germination, it seems a seed would be advantaged by small size, and associated ease of dispersal. For wind dispersed seeds, appendages such as wings or plumes increase resistance to the air and thus the chances of lateral transportation on wind currents (Fenner 1985). In the same way, fleshy pericarps or distinctively coloured fruits or arils attract particular dispersers.

The mechanism of dispersal is related to the nature of the dispersal unit. The large diaspores of *Idiospermum australiense* have no known dispersers except the force of gravity. Other relatively large fruits are animal dispersed, while many of the smaller and

lighter diaspores are associated with wind dispersal. There is evidence that animal dispersal is more efficient than dispersal by wind (Whitmore 1984). Over 90% of the species in this investigation were animal dispersed species, and the remainder were dispersed by wind.

The relationship between animal dispersers and the diaspores they disperse is mutualistic: animals rely on the fruits or seeds as a food source, and plants rely on animals for dispersal (Willson 1992). Relationships have been established between seed size and dispersers (Howe, Schupp and Westley 1985, Hladik and Miquel 1990), and it has been postulated that seed size might be more closely associated with characteristics of dispersers than with advantageous establishment conditions (Grubb 1998).

Dispersal agents and light requirements for germination

The range of animal dispersers in the Australian tropical rainforests includes bats, birds, including the large cassowary, the musky rat kangaroo, possums, uromys and melomys and other rodents. Despite larger fruits being supposedly less easily dispersed, the usually fleshy nature of these fruits is itself an attractant to dispersers (Jones and Crome 1990) so the issue might be more accurately one of the distance of dispersal of large fruits.

It is interesting that a number of the species which have a requirement for light with a high R:FR ratio or avoidance of light with a low R:FR ratio for germination are understory species at least in some situations (*Antirhea tenuiflora, Gardenia ovularis, Lasianthus strigosus, Pittosporum venulosum, Pittosporum wingii, Ptychosperma elegans, Synima cordierorum).* Efficient dispersal would seem to be especially important for regeneration in these species, and this is associated with avian dispersal in all instances.

There is an obvious association between the largest fruits and the cassowary, although smaller fruits are also consumed and dispersed by this bird as is evidenced in cassowary droppings (Stocker and Irvine 1983). Coppery brushtail possums and rodents also disperse some large fleshy fruits, sometimes in association with flesh consumption, also

in caching for future consumption. Bats consume large fleshy fruits, dropping the seed beneath a perch, or while in flight (A.K. Irvine pers.comm.).

In this study, approximately 90% of the species have fleshy fruit, slightly higher than the 84% of 774 species reported by Hyland (1982) and within the range of 75%-95% estimated by Webb and Tracey (1981). Disruption of the relationship between diaspores and dispersers can have dramatic effects on either population.

Very hard coated seeds tend to be associated with rodents, some of which are capable of chewing through the seed coat to consume all or part of the seed, while others use the seed coat to wear down their constantly growing incisors (A.K. Irvine pers.comm.) The timing of dispersal is significant in terms of the availability of dispersers; germination success should be enhanced by the coincidence of seed maturation and dispersal agents. However, any suggestion that the availability of dispersers influences fruiting patterns is probably unrealistic, since phenological events prior to dispersal (flowering, pollination, fruit set) would have to be similarly influenced, and this is unlikely (Herrera 1985; Gautier-Hion 1990).

Reports from the neotropics indicate that wind dispersed seeds are shed during the dry season, when winds are strong and deciduous trees have shed their leaves (Foster 1982; Augspurger 1984). For the wind dispersed north Queensland species in this study, most were collected near the beginning of, or early in the wet season when moisture is not limiting for germination. It has been noted earlier that almost all these seeds lack a light requirement for germination, and germinate rapidly after dispersal. The exceptions were *Parsonsia latifolia* and *Syncarpia glomulifera* which were collected in the drier season and took five weeks and one week respectively to initiate germination, and which did not germinate in green light (simulated canopy shade).

The dehiscent fruits of the samara-producing species, most of which are canopy or emergent trees, are well placed to disperse their seeds in the wind, and yet it seems that they are not carried far, but tend to produce a concentration of seeds close to the parent plant (Janzen 1975; B. Hyland, pers. comm. for *Cardwellia sublimis*). As has been shown, these are all capable of germinating in the forest shade. The plasticity in light requirements for germination of most of the wind dispersed seeds, as for those species

with no apparent means of dispersal (autochorous seeds), may in part explain the apparent lack of dependency on animal dispersers (Hladik and Miquel 1990).

Maternal light environment

Although it is possible to describe the situations in which the maternal light environment could influence germination response to light quality, this investigation did not allow identification of these cases. Consequently, it is only possible to speculate on when such conditions might apply to the species in this study. Future studies are needed to explore this subject in greater depth.

Phytochrome is synthesised during embryogenesis and exists in the Pr or Pfr form depending on the spectral quality of the light that reaches it. This spectral quality is determined by the absorptive properties of the tissues surrounding the diaspore, and whether maturation occurred in the shade of green leaves, which strongly absorb red light (Casal and Sanchez 1998).

In the same way that canopy shade reduces the R:FR ratio of light, chlorophyll in the tissues surrounding the embryo affects light quality (Cresswell and Grime 1981). Since the photoconversion of phytochrome between Pr and Pfr occurs only when the seed is moist (Cresswell and Grime 1981), the timing of chlorophyll loss in relation to drying of the seed is clearly important. The relative proportions of the two forms of phytochrome in a seed remain as they were when the seed dried out. It was not possible to determine when and if this occurred for the species studied.

Varying germination responses to light quality seen both between seeds from the same parent tree and within populations of a species are explicable in terms of different genotypes and the differing microclimates in which the seeds develop. The position of a seed within a fruit, or the position of a fruit on a tree can result in a difference in the quality of light incident on the seed, as can the age of the seed. The same effect can result from differing rates of chlorophyll loss or drying out (Wulff 1995). The resultant heteroblasty can be seen to be ecologically advantageous in the unpredictable

environments encountered by seeds in the tropical rainforest or any other natural environment (Gutterman 1992).

In this study, since all seeds were kept in darkness between collection and sowing, the effect of the maternal light environment might have been lost by dark reversion of Pfr to Pr, at least for some species. However, since PhyB is known to be photo stable (Furuya 1993), and has been shown to exist in the dark germinating seeds of experimental species, it is reasonable to suggest that the species which germinated in darkness in this study might have done so under the influence of the maternal light environment.

Apart from the species in Group 7 that did not display a germination response to the light environment, significant germination in darkness was observed in Group 3 species with maximum germination in darkness, Group 4 species (minimum germination in white light), and Group 5 species (minimum germination in green light). The negatively photoblastic characteristics of species in Groups 3 and 4 distort interpretation or speculation about the effects of the maternal light environment. Species in Group 5 could theoretically be responding to the maternal light environment in their avoidance of light with a low R:FR ratio.

It might also be hypothesised that the failure of the Group 1 species (*Alpinia arctiflora, Alpinia caerulea, Archirhodomyrtus beckleri, Casearia* sp., *Diplocyclos palmatus, Lasianthus strigosus* and *Pittosporum wingii*) to germinate in darkness might reflect a maternal light environment with a low R:FR ratio, such as occurs when seeds mature surrounded by green maternal tissue until they dry out. Following such speculation, the green seed of *Micromelum minutum* might be expected to have a requirement for light with a high R:FR ratio, but this seed, which does not dry out, germinated freely and rapidly in all light environments. In contrast, the seeds of *Evodiella muelleri* are matured within green fruit tissues, and were able to germinate in light with both high and low R:FR ratios (white and green light), but not in darkness.

The lack of a light requirement for germination in the samaras of the Proteaceae can possibly be explained in terms of the maternal light environment. The follicles of these species, usually held aloft in open sunlight, are green until they approach maturity, at which time they dry out and turn brown. It is possible that red light is able to penetrate

the drying follicle, promoting Pfr formation in the seeds so that on release they contain sufficient Pfr for germination. Alternatively, the short burst of sunlight received by the seeds when the follicle dehisces might be sufficient to induce germination. In the absence of knowledge of when the optical properties of the maternal tissues changed in relation to seed maturity, and other relevant factors, substantial further investigation would be required to verify the truth or otherwise of these speculations.

General Conclusions

While the results of this investigation pertain only to the species studied in the conditions of this study, they have application as guidelines to what might be expected in the same or related species in similar conditions. One hundred and six species of the north Queensland tropical rainforest were categorised according to time to initiation of germination, uniformity and capacity of germination.

The most common strategy observed in this study was rapid germination (within six weeks of sowing) accompanied by high uniformity and capacity of germination. Next in terms of frequency was rapid germination with intermediate uniformity and high capacity, and lastly, both rapid and delayed (>6 weeks) initiation of germination with a lack of uniformity and low capacity. Lack of uniformity (differential dormancy), while a less common strategy, has the advantage of spreading germination in time and potentially in space. Uniformity and capacity of germination, which are not usually quantified in germination studies, are useful data for maximisation of effective operations in revegetation activities.

Refinements to determination of the time to germination have been seen to be possible and desirable. Since the fleshy recalcitrant seeds of non-pioneer species do not dry out, embryonic development would continue from the time of dispersal to germination (Vasquez-Yanes and Orozco-Segovia 1990). This suggests that a more accurate measure of time to germination would be achieved by collecting such seeds directly from the parent tree, and avoiding fallen fruit. The time to germination should then be measured as the time from collection to germination, rather than the time of sowing to germination as was the case in this study.

Germination responses to light quality were recorded for 87 seed lots. For the first time, the germination responses to three ecologically relevant light environments were presented in a graphical form demonstrating the relative levels of germination in each treatment. Results indicated that for the majority of species germination was not affected by the spectral quality of the light environment. Species with a light response tended to fall into definable groups which were represented graphically in a conceptual framework (a ternary plot) showing germination not only in relation to all three

ecologically relevant light environments, but also in relation to the other species. The groups identified species with a total or partial requirement for light with a high R:FR ratio, species with maximisation of germination in darkness, and those with minimum germination in white, green and black light. Significantly, there were no species with maximum germination in green light. This knowledge, previously undocumented, suggests further guidelines for optimising returns in nursery germination and direct seeding for revegetation and rehabilitation of tropical rainforests.

Seed size was shown to be weakly associated with germination in white light for all species in the study. At the family and genus level, observations confirmed this trend, except for the negatively photoblastic species, in which the response was reversed. Fruits with more than one seed were seen to be predominant in species with maximum germination in light with a high R:FR ratio and those with minimum germination in light with a low R:FR ratio.

Dispersal for both light responsive and nonresponsive species was seen to be predominantly by birds, often in association with other animal dispersers (A.K. Irvine pers. comm., pers.obs.). Wind dispersed species were generally not responsive to light quality at germination. The two wind dispersed species that demonstrated a light requirement were suited by morphology (*Parsonsia latifolia*) or distribution (*Syncarpia glomulifera*) to this less efficient mode of dispersal.

Recommendations for future study

Repetition of this study over a number of years, with the addition of seedlots from different provenances, would authenticate the findings and also indicate the degree of intraspecific variation which might exist in relation to both time to germination and response to light quality. Additional species should also be incorporated to validate and expand the results found in this study.

Ideally, studies of germination responses in varying light environments should be conducted in the field as well as in the shadehouse. Germination studies under natural conditions in the forest environment are important, but the difficulty of such studies lies in measuring the spectral quality of light at the location of the seed, and in segregating light effects from other environmental effects. Nevertheless, field studies are suggested for comparison of results with those of shadehouse experimentation.

Time to initiation of germination was used in this study to compare responses between species for the duration of the investigation. It is suggested that germination should be studied over time until all viable seeds have germinated. This would provide results which are a more accurate reflection of germination strategies, and which can be compared to the various measurements of germination published by other authors. Further studies to determine the constancy of uniformity and capacity of germination for each species would be helpful. If these characteristics could be shown to be predictable, the efficacy of revegetation work would be enhanced.

In this study, it was only possible to speculate on the effects of extra-embryonic tissue on the light reaching the embryo. Future studies exposing excised embryos to varying light environments would provide interesting results on the exact nature of the species' germination response without interference from surrounding tissues. This could then be compared with results achieved by experimentation with intact fruits and/or seeds under the same light conditions.

There is a possibility that some species collected at the same time exhibit similar germination strategies. For example, many species collected in the cooler months, which are also the drier months, failed to germinate during the course of this study.

Eleven of the species with a germination response to light quality were collected in the month of March. Future investigations might reveal seasonal patterns of behaviour common to groups of species.

Other suggestions for future studies have been included in the earlier chapters. It seems that because of the limited documentation of germination strategies of species of tropical rainforests of north Queensland, almost every aspect of investigation suggests further areas of study.

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