PHENOLOGY AND GERMINATION IN SOME RAINFOREST CANOPY SPECIES AT MT FIELD NATIONAL PARK, TASMANIA

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(with five tables and three text-figures)

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The timing of shoot expansion, flowering, germination and leaf fall was recorded in some rainforest canopy species at Mt Field National Park, Tasmania. Seed collected from these and two other species was germinated in Hobart under controlled conditions. Most of the variation in phenology and germination requirements was continuous and correlated broadly with distribution with respect to the temperature climate. The species which commonly occur at high altitudes — *Athrotaxis selaginoides*, *A. cupressoides*, *Nothofagus gunnii* and *N. cunninghamii* — germinated earlier at low temperatures than the others, with provenance variation indicated in *N. cunninghamii*. The cold-sensitive species *Atherosperma moschatum* failed to germinate at low temperatures, with a secondary dormancy indicated. *Atherosperma moschatum* and *Phyllocladus aspleniifolius* showed delayed shoot expansion during the cool growing season of 1984–85 which rendered the shoots more frost-sensitive. The periodicity of seed production is also greatest in the high altitude species, although the ecological implications are uncertain with respect to climate. Only *P. aspleniifolius* shows evidence of prolonged seed dormancy. This characteristic enables the populations to survive large-scale disturbance as soil-stored seed and therefore is an important feature of the regeneration ecology of this species.
Key Words: germination, phenology, *Atherosperma*, *Athrotaxis*, *Eucryphia*, *Nothofagus*, *Phyllocladus*, Tasmania.

INTRODUCTION

Although rainforest forms one of the major vegetation types in Tasmania, relatively little of the basic biology of the component species is documented, other than autecological studies of *Nothofagus cunninghamii* (Hook.) Oerst. (Howard 1973a,b,c) and a study of germination and dispersal in *N. cunninghamii*, *Eucryphia lucida* (Labill.) Baill. and *Atherosperma moschatum* Labill. (Hickey *et al.* 1983). Read & Hill (1985, 1988a) have described regeneration patterns in the major canopy species, *N. cunninghamii*, *A. moschatum*, *E. lucida*, *Athrotaxis selaginoides* D. Don and *Phyllocladus aspleniifolius* (Labill.) Hook. f. They noted differences among the species in their gap requirement for regeneration and modes of reproduction which have a large impact on the forest dynamics and community composition. The large gap requirement of *P. aspleniifolius* and *A. selaginoides* is of particular interest, since regeneration in closed forests by these species is commonly insufficient to maintain their continued presence in such forests, although they may currently form a major component of the forest canopy (Ogden 1978, Cullen 1987a,b, Read & Hill 1988a). Similar population dynamics have been recorded in *Athrotaxis cupressoides* D. Don (Ogden 1978) and *Nothofagus gunnii* (Hook. f.) Oerst. (Read & Hill 1988a, unpubl. data). The occurrence of these species with respect to altitude and climate, summarised in table 1, has been discussed by Read & Hill (1988b) and Cullen (1987a,b).

Temperate trees have a limited growing season in natural conditions and there is considerable variation among species in the timing and patterns of foliage expansion and the timing of flowering and seed release (e.g. Wareing 1956, Bussell 1968). Variation may also occur within a single species at different sites. Similarly, the importance of the relationships between the physical environment and seed germination in the distribution of a species in space and time, and the variability of these relationships has been noted by many authors (e.g. Grubb 1977, Bazzaz 1979). These features are examined in *Nothofagus cunninghamii*, *Eucryphia lucida*, *Atherosperma moschatum*, *Phyllocladus aspleniifolius* and *Athrotaxis selaginoides* at Mt Field National Park (42°41'S, 146°40'E), with experimental germination studies on seed collected from these species, as well as from *Nothofagus gunnii* and *Athrotaxis cupressoides*, in order to determine whether differences among species in phenology and germination characteristics may

TABLE 1

Summary of the Distribution of some Rainforest Canopy Species with Respect to Altitude in Tasmania

Species	Altitudinal occurrence	
	Range (m a.s.l.)	% of records over 800 m a.s.l.*
Atherosperma moschatum	0–1120	12
Athrotaxis cupressoides	600–1330	93
A. selaginoides	20–1300	56
Eucryphia lucida	0–1000	3
Nothofagus cunninghamii	0–1260	27
N. gunnii	550–1260	88
Phyllocladus aspleniifolius	0–1160	25

* The percentages refer to records from surveys and herbarium collections (data supplied by M.J. Brown, J.R. Busby and the Tasmanian Herbarium), and do not necessarily reflect stem frequency over these altitudes.

TABLE 2

Species, Site Locations and Phenological Features recorded at Mt Field National Park

Altitude (m a.s.l.)	Species	Observations
180	*Atherosperma moschatum* *Nothofagus cunninghamii*	Leaf expansion: 1982–83, observations fortnightly
700	*A. moschatum* *Eucryphia lucida* *N. cunninghamii* *Phyllocladus aspleniifolius*	Leaf expansion: 1982–83, observations fortnightly. Flowering*, seeding and germination: 1982, 1984 and 1985, observations monthly, but with some gaps in the observation period.
920	*A. moschatum* *Athrotaxis selaginoides* *N. cunninghamii* *P. aspleniifolius*	Leaf expansion: 1982–83, observations fortnightly. Flowering*, seeding and germination: 1982, 1984 and 1985, observations monthly with some gaps in the observation period.
980	*A. selaginoides* *N. cunninghamii*	Leaf expansion: 1982–83, observations fortnightly.

* The presence/absence of flowering was noted annually from 1982–88.

contribute to the observed patterns of species regeneration and distribution.

METHODS

Phenology

Four sites were selected at Mt Field over an altitudinal range of 800 m, from 180 m a.s.l. to 980 m a.s.l. The species observed at each site and the features recorded are listed in table 2. Sites 1–4 were observed from May 1982 to May 1983 at fortnightly intervals. Sites 2 and 3 were also observed from August 1984 to August 1985 at monthly intervals. At each site, five lateral branches were tagged on three trees of each species on exposed forest edges. Saplings (originated from seed) of *Nothofagus cunninghamii*, *Eucryphia lucida* and *Phyllocladus aspleniifolius* were also tagged at Site 2. No saplings of seedling origin were found in *Atherosperma moschatum* at this site. The following features were recorded:
(1) the timing of bud-break;
(2) leaf production and abscission;
(3) the time of flowering, seeding and germination (where possible); germination is often difficult to record directly in the field, and here is recorded indirectly as the first appearance of cotyledonary seedlings.

Growth patterns were also observed fortnightly from 1982 to 1985 in seedlings raised in Hobart from seed or cotyledonary seedlings collected from Mt Field in June 1982. One group of five seedlings of each species was grown outside under natural daylengths, and another group of seedlings was grown in a glasshouse under natural daylengths.

Germination

Seed was collected from Mt Field in 1982, a year of exceptionally high seed production for all of these species, from three trees each of *Nothofagus cunninghamii* (Nc700), *Eucryphia lucida*, *Phyllocladus aspleniifolius* and *Atherosperma moschatum* at 700 m a.s.l. and from *N. cunninghamii* (Nc980), *N. gunnii*, *Athrotaxis selaginoides* and *A. cupressoides* at 980 m a.s.l. All seeds were collected and sown in 1982 following dry storage at room temperature. Poorly developed seeds of *A. moschatum* and *Athrotaxis* spp. were discarded, and therefore the final germination percentages do not reflect the overall viability of the seed crop.

The seed treatments for each species were as follows:
(1) incubated moist in light at 4°, 12°, 17°, 25° and 32°C;
(2) incubated moist in dark conditions at 25°C;
(3) incubated moist in light at 4°C for four weeks, followed by 25°C.
The failure of *Phyllocladus aspleniifolius* to germinate in any of the above treatments led to the following treatments for this species only:
(4) seed soaked for 24 hours in HCl (pH 2) followed by incubation moist in light at 20°C;
(5) seed scarified and incubated moist in light at 20°C;
(6) seed coat removed and seed incubated moist in light at 20°C;
(7) seed boiled for 5 minutes then incubated moist in light at 20°C;
(8) seed sown in pots of sandy loam and placed outside in full sunlight, with daily watering.

In treatments 1 to 7, 30–40 seeds of each tree were placed in a petri dish on a pad of Whatman's Seed Test Thick filter paper (three dishes per species for each treatment, one for each parent tree). "Thiram" fungicide was dusted on the seed pad prior to the addition of distilled water. The petri dishes were incubated in controlled environment growth cabinets under incandescent and fluorescent lights (150 μmol quanta $m^{-2}s^{-1}$). The "dark" treatment was provided by cardboard boxes lined with black cartridge paper and seeds placed in this treatment were sown and observed under green light.

Results were observed every 1–2 days for the first 50 days, then every 3–5 days until Day 100, followed by irregular observations. Observations of treatments 1–3 were continued for 25 days after the last seed germinated. Observations of the 12°C treatment ceased after 125 days, due to fungal infection of the remaining seeds. Observations of treatments 4–7 were discontinued after 90 days. Treatment 8 was observed for 30 months.

RESULTS

Bud-break and Shoot Expansion

The uppermost bud on *Nothofagus cunninghamii* shoots is lateral rather than apical, with the new branch rotating to appear apical (Howard 1973b). The overwintering buds are sheathed by bracts, whereas in *Eucryphia lucida* the buds are enclosed in a yellow wax. Apical buds of the other

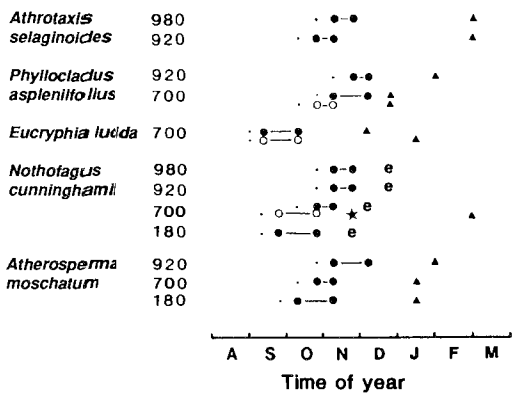

FIG. 1 —Timing of leaf production at Mt Field at each altitude, examined at two-week intervals in 1982–83.

●—● *The period during which bud-break occurred in mature plants*

○—○ *The period during which bud-break occurred in saplings (of seedling origin) 1–1.5 m high.*

The dots (•) preceding the marked period indicate the time of the previous observation. Most Nothofagus cunninghamii *leaves were produced during the spring growth flush, but some expanded shoots of saplings continued to produce new leaves at the apices.*

e *The date at which* N. cunninghamii *leaves were fully expanded.*

★ *The date at which* N. cunninghamii *leaves produced in the spring growth flush were fully expanded, with further leaf production occurring at the shoot apices or in later growth flush.*

▲ *The date by which leaf production had ceased.*

species are protected to some extent by the infolding of older leaves, and in *Phyllocladus aspleniifolius* by bud scales.

Bud-break occurred later with increasing altitude in all species except in *Nothofagus cunninghamii* at 920 m and 980 m (fig. 1). There was no distinct pattern in the timing of bud-break among species, other than the later bud-break of *Phyllocladus aspleniifolius* compared with other species. At 180 m a.s.l. *N. cunninghamii* buds broke earlier than those of *Atherosperma moschatum*, but there was no difference in timing between these species at 700 m a.s.l. and 920 m a.s.l. Similarly, *Athrotaxis selaginoides* buds opened earlier than those of *N. cunninghamii* at 920 m a.s.l. but there was no difference among these species at 980 m a.s.l. Bud-break occurred up to 2–4 weeks earlier in saplings of *P. aspleniifolius* and *N. cunninghamii* at 700 m a.s.l. than in adults. In 1984, bud-break was delayed in *A. moschatum* and *P. aspleniifolius*, so that at the 920 m a.s.l. site, leaves of these species were not fully expanded and hardened by June 1985 (Read & Hill 1988b). In contrast, leaves of the other species were fully expanded and hardened by late summer–early autumn (Read & Hill 1988b).

Nothofagus cunninghamii shoots from saplings and mature plants showed predominantly determinate growth, with a single flush of growth from axillary buds during the spring, bearing 5–16 leaves. This growth pattern is similar to that described in detail by Howard (1973b) in *N. cunninghamii* in Victoria. Many terminal axillary buds remained dormant for the whole observation period. Axillary buds formed during the growth flush occasionally broke dormancy in saplings at 180 m a.s.l. and 700 m a.s.l. during the late summer to form a second growth flush; occasional sapling shoots produced leaves continuously. Determinate shoots were fully expanded within 4–6 weeks at all sites and leaves were fully expanded within 6–8 weeks (fig. 1). *N. cunninghamii* seedlings which had germinated in Hobart in June 1982 showed continuous apical growth in the glasshouse during winter, and axillary buds broke in August. Seedlings growing outside in August showed some apical growth through winter, with axillary buds breaking in October. Subsequent growth in seedlings, both inside and outside the glasshouse, was a combination of growth flushes from axillary buds and continuous apical growth until early autumn. Growth then ceased outside the glasshouse but continued inside the glasshouse, both by continuous apical growth and occasional flushes from dormant axillary buds, with a major period of determinate growth soon after daylength began increasing in winter. This pattern of growth, with slight variations in timing from year to year, was observed in the same seedlings until observations ceased in October 1985.

All other species produced foliage indeterminately. *Atherosperma moschatum* and *Eucryphia lucida* usually produced 2–4 leaves on each shoot during the growing season at Mt Field. *Phyllocladus aspleniifolius* usually produced a single whorl of 5–7 phylloclades (mostly determinate). The *Athrotaxis selaginoides* shoots produced 11–23 leaves. Leaf production in mature plants of *A. selaginoides*, *A. moschatum*, *E. lucida* and *P. aspleniifolius* ceased during summer and

did not resume until the following spring. Leaf production ceased later at the higher altitudes (fig. 1). In seedlings raised in Hobart, leaf production was continuous in the glasshouse, and continued very slowly outside the glasshouse during the first winter after germination. In later years, growth continued until May outside the glasshouse, then did not resume until October. These growth patterns remained constant until observations ceased in October 1985, with slight variation in timing from year to year.

The foliage of *Phyllocladus aspleniifolius* seedlings at Mt Field consisted entirely of leaves for the first two to three years of growth, but seedlings of the same age which were grown outdoors in Hobart (with a faster growth rate) produced phylloclades within six months.

No leaf loss was recorded in any of these species other than due to browsing. Therefore the leaf life span was greater than 41 months.

Flowering, Seeding and Germination at Mt Field

In 1984–85, flowering and seed maturation of *Eucryphia lucida* were delayed (figs 2 & 3). Seed maturation and germination were also delayed in *Atherosperma moschatum* in 1984–85, and flowering in this species was delayed in 1985 (figs 2 & 3). These delays coincided with the slightly lower temperatures of the 1984–85 growing season. Bureau of Meteorology records at Maydena (42°46'S, 146°36'E, 267 m a.s.l.) show mean monthly temperatures from November to February averaging 20.4°C in 1983–84, compared with 19.4°C in 1984–85. The timing of cone development in *Phyllocladus aspleniifolius* was not delayed but seed maturation at 920 m a.s.l. was late (fig. 3). The flowering period of *E. lucida* is long relative to that of *A. moschatum* (fig. 2). However, the pollination period may be narrowed by the behaviour of the insect pollinators.

Flowering and seeding of *Nothofagus cunninghamii* and *Athrotaxis selaginoides* at Mt Field were recorded only in the 1981–82 growing season, which was a season of prolific seed production for all the species in this study. Occasional empty cupules of *N. cunninghamii* were observed in subsequent years, indicating that flowering was occurring in this species at a very low frequency. No viable seeds were found. However, cone development was recorded in *Athrotaxis* species in late September 1988, and also

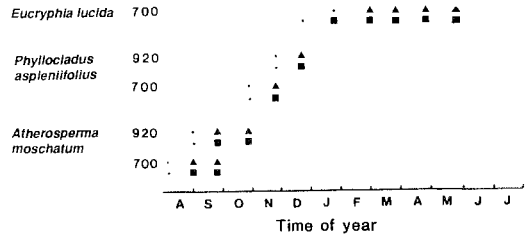

FIG. 2 — Timing of flowering at Mt Field at each altitude, examined at monthly intervals in 1983–84 (■) and 1984–85 (▲). Flowering was not observed in A. selaginoides *and* Nothofagus cunninghamii *during this period. The dots (•) preceding the marked period indicate the date of the preceding observation. The date shown for* Phyllocladus aspleniifolius *indicates only the first appearance of the cones. The dates shown for both* P. aspleniifolius *and* Atherosperma moschatum *refer only to the appearance of female cones/flowers.*

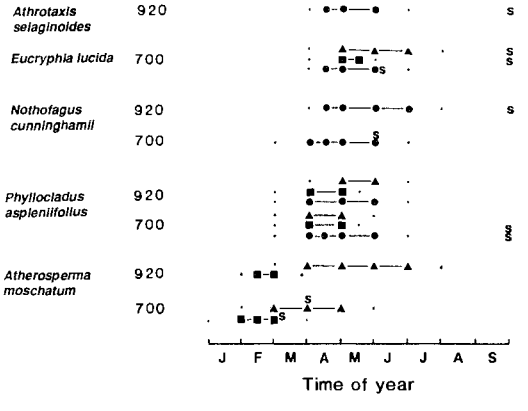

FIG. 3 — Timing of the period of seed maturation and release (● 1982; ■ 1984; ▲ 1985), and the first appearance of seedlings (s) at Mt Field at each study site, examined at two- or four-week intervals. The dots (•) indicate the dates of observations prior to seed maturation and following the majority of seed release.

heavy flowering of *N. cunninghamii* and *N. gunnii* in October and November respectively, with indications of a year of heavy seeding for both genera. *Atherosperma moschatum* and *Eucryphia lucida* flowered prolifically each year and *Phyllocladus aspleniifolius* produced cones each year, but most prolifically in the 1981–82 growth season and again in 1988–89.

Germination of *Nothofagus cunninghamii* was recorded during autumn at 180 m a.s.l. and 700 m a.s.l. in 1982, with seedlings not apparent until spring at 920 m a.s.l. and 980 m a.s.l. (fig. 3). *Athrotaxis selaginoides* seedlings did not appear until spring in 1982. *Eucryphia lucida* was only studied at 700 m a.s.l. at Mt Field, with autumn germination recorded in 1982 and spring germination in 1984 and 1985. *E. lucida* seed does not mature until the autumn following the year of flowering. *Atherosperma moschatum* seedlings appeared in autumn at 180 m a.s.l. and 700 m a.s.l. At 920 m a.s.l. seeding was profuse, and seed collected in March 1985 was germinated in the laboratory with 92% viability of well-formed seed, which was equivalent to 36% of the total seed collected. However, successful field germination of *A. moschatum* was very rare at this site. Many hundreds of well-formed seeds were observed close to the parent trees, but only two cotyledonary seedlings were recorded, germinating in September. Although many seeds remained intact after winter, no further germination was observed. Cotyledonary seedlings of *Phyllocladus aspleniifolius* appeared in spring at 700 m a.s.l. The seed crop of *P. aspleniifolius* at 920 m a.s.l. was small, except in 1982, and no seedlings were observed at this site.

Experimental Germination

Phyllocladus aspleniifolius seed did not germinate under treatments 1–3. The other species germinated readily under these treatment conditions (table 3). The germination score for these species at 25°C was unaffected by the light conditions (table 3). The onset of germination was most rapid and the time taken to reach 50% of the final germination score shortest at 25°C for all species, although with little difference at 17°C (tables 3 & 4). Incubation temperature did not affect the final germination percentage, other than at 32°C, where no germination occurred and seed had deteriorated after 28 days, and at 4°C in *Atherosperma moschatum* (table 3). At 12°C a substantial proportion of seeds of *Nothofagus cunninghamii*, *A. moschatum* and *Eucryphia lucida* were infected by fungus after 125 days (tables 3 &4) and scoring was abandoned. The final germination percentage is assumed to be the same as at 25, 17 and 4°C for *N. cunninghamii* and *E. lucida*. However, since *A. moschatum* failed to germinate at 4°C, the

TABLE 3

Final Germination Percentages of each Species*

Species	Site (m a.s.l.)	Incubation temperature (°C)						
		32	25 light	25 dark	17	12	4	4–25†
Nothofagus cunninghamii	700	0	21	20	22	12‡	24	25
	980	0	48	50	48	26‡	51	46
N. gunnii	980	0	43	40	36	39	41	40
Eucryphia lucida	700	0	93	91	93	60‡	95	93
Atherosperma moschatum§	700	0	92	97	93	49‡	0	99
Athrotaxis selaginoides§	980	0	61	59	63	60	67	63
A. cupressoides§	980	0	51	52	57	57	57	51

* Each percentage value is the mean of results of seed from three trees at the same site.
† 4°C for 4 weeks, then incubated at 25°C.
‡ The final count was at 125 days, with remaining seeds infected by fungus.
§ Poorly formed seeds (small, shrivelled or discoloured) were not included.

reduced germination score of *A. moschatum* at 12°C may be due to factors other than fungal infection. Differences among trees in germination rate were small. Variation in viability ranged from 3% of the mean value in *A. moschatum* to 19% in *N. cunninghamii*.

The 4°C pre-treatment increased the rate of germination for *Eucryphia lucida*, *Nothofagus gunnii* and *Athrotaxis selaginoides* (table 4) but had no effect on the final germination percentage of any species (table 3). *N. gunnii*, *A. selaginoides* and *A. cupressoides* germinated earlier at 4°C than the other species (table 5), including Nc980, and germination of these species was complete within 125 days at 12°C (tables 3 & 4). *N. cunninghamii* seed collected at 980 m a s.l. germinated more rapidly at 12°C and 4°C than seed collected from 700 m a s.l. (tables 4 & 5).

Phyllocladus aspleniifolius failed to germinate in Treatments 1–7, although seeds had fully imbibed water within 24 hours. Observations on Treatment 3 ceased on Day 151 due to fungal attack, and on Day 125 for the other treatments. However, seeds germinated in soil placed in the open air with daily watering (Treatment 8) in the spring of 1983, i.e. after two winters. Seedlings appeared in September and there were no later germinations, with a final germination percentage of 62%.

Seed of *Nothofagus cunninghamii*, *N. gunnii*, *Eucryphia lucida*, *Athrotaxis selaginoides* and *A. cupressoides* stored dry at room temperature germinated with 50–80% viability after 32 months. Seed of *Atherosperma moschatum* could not be germinated at 20°C under a 24-hour photoperiod after two months dry storage at room temperature. Seed of *A. moschatum* stored dry at 4°C was successfully germinated at its original level of viability after four months, but with only 3% germination after five months storage. However, the embryo appeared healthy in both cases of germination failure and seed stored in these conditions germinated (96%) after incubation in darkness at 20°C.

DISCUSSION

Phenology

The patterns of shoot growth in *Nothofagus cunninghamii* are identical to those recorded in Victoria by Howard (1973b), although the appearance of a second growth flush in *N. cunninghamii* appears to be more frequent in Victoria than at Mt Field. Howard noted that the incidence of a second flush decreased with increasing altitude at Mt Donna Buang, and therefore the occasional occurrence of a second growth flush at low altitudes at Mt Field and the absence of this feature at high altitudes probably reflects the cooler

TABLE 4

The Number of Days to the Onset of Germination and to reach 50% of the Final Germination Percentage, expressed as a Range

Species	Site (m a.s.l.)	Incubation temperature (°C)			
		25	17	12	4–25*
Nothofagus cunninghamii	700	7–9	9–11	23–125†	7–10
	980	5–6	7–8	14–115†	4–7
N. gunnii	980	7–9	10–12	14–40	1–7
Eucryphia lucida	700	7–15	12–25	23–115†	1–1
Atherosperma moschatum	700	7–10	11–13	26–70†	9–11
Athrotaxis selaginoides	980	8–15	13–23	20–80	1–8
A. cupressoides	980	8–22	10–24	20–85	5–10

* 4°C for 4 weeks, then incubated at 25°C.

† Final germination percentage is assumed to be the same as at 25°C.

TABLE 5

Cumulative Percentages of Laboratory Germination at 4°C

Species	Site m a.s.l.	Days from sowing				
		129	136	140	151	223
Nothofagus cunninghamii	700	0	0	0	1	24
	980	0	0	0	19	51
N. gunnii	980	24	40			
Eucryphia lucida	700	0	0	0	0	95
Atherosperma moschatum	700	0	0	0	0	
Athrotaxis selaginoides	980	0	9	17	67	
A. cupressoides	980	0	7	16	50	54

growing seasons. The only feature of the timing of bud-break that may be differentially limiting to regeneration and geographic distribution of species is the delaying effect of a cool growing season on the shoot expansion of *Atherosperma moschatum* and *Phyllocladus aspleniifolius*, so that these leaves may be susceptible to frost damage (Read & Hill 1988b).

The periodicity of seedfall in *Nothofagus cunninghamii* and *Athrotaxis selaginoides* has implications for regeneration of these species. Hickey *et al.* (1983) recorded seedfall of *N. cunninghamii*, *Atherosperma moschatum* and *Eucryphia lucida* at two sites in northwestern Tasmania from 1975 to 1981, summarising *N. cunninghamii* seedfall back to 1963. These data, plus data from subsequent years (J. Hickey, pers. comm.), indicate sporadic production of seed in *N. cunninghamii*, with heavy falls in 1967, 1969, 1971, 1975, 1977, 1980, 1982 and 1986 interspersed with years of low or moderate seedfall. They did not find any clear relationship between seed production and the temperature of the preceding growing season, but noted that the pattern of seed production was consistent at several sites around Tasmania. Poor seed production in 1986 at Mt Field, however, may be the result of climatic differences. Periodicity of seeding is a common characteristic of *Nothofagus* throughout its geographic range (Wardle 1984) and may allow a greater proportion of seeds and seedlings to escape predation by herbivores (Ash 1982). The time of flowering and seed release reported by Hickey *et al.* (1983) is, in general, earlier than that recorded at Mt Field and probably reflects the cooler climate at Mt Field. The sporadic nature of seed production of *N. cunninghamii* and *Athrotaxis selaginoides*, also observed in the congenerics *N. gunnii* and *A. cupressoides*, and to a lesser extent in *Phyllocladus aspleniifolius* (J. Hickey, pers. comm.), and the association of low seed viability with the years of low seed production (Howard 1973b, Hickey *et al.* 1983) must have a detrimental effect on the colonisation by these species of sites which are disturbed during periods of low seed production. For example, mixed forest burnt in western Tasmania in 1982 had a high seedling density of *N. cunninghamii* by spring 1982 (Hill & Read 1984). If this fire had burnt after 1982, the *Nothofagus* component of the mature stand developing after the fire would probably be very much lower, due to the absence of seed during the early stage of site colonisation, with site pre-emption by other species, particularly the rapidly-growing sclerophyll species. Similarly in *A. selaginoides*, which is relatively drought sensitive (unpubl. data), establishment depends on the coincidence of a good seed year with moist conditions. The infrequency of seeding in *A. selaginoides* and the drought sensitivity of seedlings must limit its ability to colonise disturbed sites, including canopy gaps, particularly combined with the faster growth rates of other rainforest species and rapid site pre-emption following the disturbance. The greater consistency of seedfall in *Atherosperma moschatum* and *Eucryphia lucida* has been shown quantitatively by Hickey *et al.* (1983). There are no long-term data on seedfall in *A. selaginoides*, and data collected since 1983 on *P. aspleniifolius* in northwestern Tasmania indicate some variability, with alternately poor (< 1 g m^{-2}) and moderate seedfall (J. Hickey, pers. comm.). It is notable that the species with the greatest

periodicity of seed production are those commonly occurring at high altitudes. It is not clear whether this is an evolutionary response to facilitate seedling establishment or to facilitate maximum growth during the short growing seasons, with reproduction only when there is an abundance of assimilate.

The time of field germination within a species, with respect to altitude, is probably related to differences both in the time of seed release and in the time taken for germination to occur, each affected by climate. This appears to be particularly critical in *Atherosperma moschatum*, since observations indicate that the late seed release at 920 m a.s.l. in 1985 led to a very low rate of successful field germination, although this seed was successfully germinated in the laboratory soon after its release. Since observations were made only at monthly intervals, fine-scale differences which have not been detected may exist in the onset of germination among species.

Germination Requirements

The early germination of *Nothofagus gunnii*, *Athrotaxis selaginoides* and *A. cupressoides* that was observed experimentally at low temperatures correlates with the predominantly high altitude distribution of these species. The earlier onset of germination at 12°C and 4°C of seed collected from *N. cunninghamii* at 980 m a.s.l. than of seed collected at 700 m a.s.l. is consistent with this trend. Cotyledonary seedlings of *A. selaginoides*, *A. cupressoides*, *N. gunnii* and *N. cunninghamii* were observed in September 1982 at 980 m a.s.l. at Mt Field (4–5 months after seed release) (tables 4 & 5), but the precise timing of seed release and germination is unknown. A high mortality, due to desiccation, occurred during the following summer, particularly on the more exposed microsites. Early germination may therefore be important in allowing early growth and establishment during a period of low evaporative loss, although early germination may also place the seedlings at risk from frost damage. Howard (1973b) noted that seed of *N. cunninghamii* of lowland populations in Victoria germinated soon after release in autumn, but did not germinate until spring at high altitudes. This pattern would be expected to show some annual variation, according to the timing of seed release as well as the climatic conditions following seed release. The data obtained in the present study indicate that the timing of germination in the field is due to the slow germination at low temperatures rather than any pre-chilling requirement. This feature has been previously reported in *N. cunninghamii* (Howard 1973b). The lack of any requirement for pre-chilling treatment in high altitude species has also been recorded in a study of alpine plants of the USA where only 3 out of 60 species had a chilling requirement (Amen 1966). Sayers & Ward (1966) observed that temperatures resulting in the best germination of alpine species in the USA (20–30°C) were similar to those for species native to lowlands. Similarly, in the present study germination was most rapid at 25°C for all species, with seed of all species killed by incubation at 32°C. However, ecologically significant differences may occur at a finer scale of temperatures than those tested here.

Germination failure at 30–35°C has been reported previously in *Atherosperma moschatum* by Read (1981) and in *Nothofagus cunninghamii* by Howard (1973b), although seed of *A. moschatum*, *Eucryphia lucida* and *N. cunninghamii* was successfully germinated by Hickey *et al.* (1983) in a 30°/20°C regime. The importance of high temperatures in limiting establishment from seed in the field is uncertain. Prolonged high temperatures in the range 30–35°C are unusual in the current distribution of forests containing these species, both in Victoria and Tasmania, but this feature may be relevant to the absence of these species from warmer sites.

A suitable combination of moisture and temperature is probably the most important factor determining seed germination under natural conditions (Mayer & Poljakoff-Mayber 1982). Howard (1973b) noted that suitable conditions for germination of *Nothofagus cunninghamii* occur within 8–9 months of seedfall and therefore reduction of viability with seed age is unlikely to be a limiting factor for regeneration. The same is true for *Eucryphia lucida*, *Atherosperma moschatum*, *N. gunnii*, *Athrotaxis selaginoides* and *A. cupressoides*. At low altitudes *N. cunninghamii*, *A. moschatum* and *E. lucida* germinate in autumn, within 1–2 months of seed release (fig. 3) and it is unlikely that the lack of germination recorded in dry-stored *A. moschatum* seed (also noted by Hickey *et al.* 1983)) would be a significant occurrence in the natural lowland environment. The greatly reduced germination score in apparently viable seed of *A. moschatum* at 900 m a.s.l. at Mt Field in 1985 is consistent with the secondary dormancy induced experimentally by cold moist or cold dry storage. However, in the field, cessation of dormancy was not observed to any significant degree, and it is not certain that light is the only

factor initiating release from this secondary dormancy. The environmental feature which is initiating the secondary dormancy observed at high altitudes is uncertain, since it is induced experimentally at both moderate and low temperatures and in both dry and moist conditions (except in the combination of moist, moderate temperatures). Any delay in germination will also result in greater mortality due to fungal attack (e.g. table 3) and insect attack. These characteristics may limit the ability of *A. moschatum* to colonise sites/microsites in which conditions suited to germination are consistently absent soon after seed release, e.g. at high altitudes.

The only species which may have soil-stored seed is *Phyllocladus aspleniifolius*; however, there are no data to indicate storage times of this species. *P. aspleniifolius* commonly appears on rainforest sites after fire (Kirkpatrick 1977, Hill & Read 1984); this may be the result either of soil storage and release from dormancy, whether "natural" or precipitated by the disturbance, or of efficient spatial dispersal. Kirkpatrick (1977) suggested that the early appearance of *P. aspleniifolius* on disturbed sites is due to bird dispersal. Seed of *P. aspleniifolius* has been recorded in pellets that have passed through the gut of birds, but the frequency of dispersal by animals and its effect on seed germination is uncertain for this species. The pattern of seed dormancy of *P. aspleniifolius* is similar to that of *Tasmannia lanceolata*, a species that commonly invades forest disturbances and has seeds that are commonly bird-dispersed (Read & Hill 1983). Howard (1974) noted that most *T. lanceolata* seedlings appeared 12 months after soil containing the seeds was collected from the field (18 months after the latest seedfall). She suggested that this was due to leaching of a germination inhibitor from the seed. It is likely that some dormancy mechanism is necessary to survive bird-dispersal.

Studies of the dynamics of populations of *Phyllocladus aspleniifolius* suggest that large-scale disturbance is an important feature of its regeneration (Read & Hill 1988a). Dormancy mechanisms, permitting a large soil store of seed which can survive a large-scale disturbance such as fire or severe frost, would facilitate rapid establishment, especially if the disturbance factor also precipitated release of the seed from dormancy. The infrequency of regeneration within rainforest may be related to the seed dormancy if, for example, a large canopy opening is required for dormancy release. However, Read & Hill (1988a) recorded relatively high *P. aspleniifolius* seedling densities on sites where it was failing to regenerate. Therefore it is unlikely that dormancy characteristics are directly limiting its regeneration within undisturbed rainforest, even though the percentage of its annual seed crop which germinates may possibly be small relative to that which remains dormant.

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