

## Invasion by *Pittosporum undulatum* of the Forests of Central Victoria. II\* Dispersal, Germination and Establishment

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### Abstract

Invading *Pittosporum undulatum* tends to be clumped around the butts of established trees. This is due to the preferential deposition of seeds in these sites by the European blackbird (*Turdus merula*) which is believed to be the main vector of dispersal. Native silvereyes (*Zosterops lateralis*) eat some seed but are not considered important in dispersal. The high mortality of seedlings in exposed sites reinforces the patchy pattern originally dictated by seed dispersal. Seeds may germinate after seed fall in spring but most seeds germinate in autumn. No seeds germinate during summer because of the low rainfall and high temperatures, the optimum germination temperature being 18–21 °C. After 16 months' storage at moderate temperatures and humidities, 80% of seed was still viable but viability was reduced to 30% at very low humidities. Seedlings of *P. undulatum* have three growth stages. The juvenile and transitional stages last 6–12 months and have alternate leaves. In the adult phase a terminal vegetative bud forms at the stem apex. Bud burst may occur several times a year in seedlings and twice a year in fruiting adults. The seedling root habit varies with soil type. The seedlings are able to coppice if the shoot is removed. *P. undulatum* is an aggressive invader of eucalypt forests despite the poor survival of the initial colonizers. The formation of a regeneration niche ensures the survival of succeeding generations. Consequently, *P. undulatum* is a permanent threat to the Victorian vegetation.

### Introduction

In Victoria, *Pittosporum undulatum* Vent. is invading sites to which it is not native (Gleadow and Ashton 1981). These areas include *Eucalyptus obliqua* and *E. regnans* forests in the Dandenong Ranges, *Leptospermum laevigatum* communities on the Mornington Peninsula and remnants of the *E. radiata*–*macrorrhynca*–*cephalocarpa* forests in the eastern suburbs of Melbourne. The pattern of invasion into forests of the last type is patchy, with most *P. undulatum* seedlings and trees clustering around the butts of established *Eucalyptus*, *P. undulatum* and *Exocarpos cupressiformis* trees (Gleadow and Ashton 1981). This pattern of invasion could be due to uneven seed dispersal, the microclimate required for seed germination or the range of sites in which the seedlings can establish and grow. These three hypotheses are examined in this paper.

Although the bright orange seeds of *P. undulatum* should be a good sign stimulus (Ridley 1930; van der Pijl 1972), they are not widely eaten by native birds. Pied

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currawongs (*Strepera graculina*) only eat the seed in lieu of other food (Cooper 1959; Barkly Rose 1973; R. Buchanan, personal communication) and although silvereyes (*Zosterops lateralis*) eat some *P. undulatum* seed (Gannon 1935; Cooper 1959), they are largely insectivorous (Lea and Gray 1935). On the other hand, *P. undulatum* seeds form a large part of the diet of the introduced European blackbird (*Turdus merula*) during winter. *P. undulatum* may be behaving as a weed because such a dispersal vector has been introduced. In New Zealand, seeds of the native *Pittosporum* species are also eaten to some extent by possums (*Trichosurus vulpecula*) (Ridley 1930), but this has not been documented in Australia. Seeds collected from the droppings of blackbirds, silvereyes and possums were tested to see if any of these could act as a dispersal vector. Pied currawongs were excluded from the survey because they are not well established in the Melbourne area (Anon. 1976).

Blackbirds tend to eat only fresh seeds, and seeds that are not eaten fall to the ground. The factors affecting the longevity of seeds under various environmental conditions were studied in conjunction with observations of naturally emerging seedlings in the field. The conditions required for germination were also delineated.

The pattern of *P. undulatum* in open forests may also reflect the distribution of microsites suitable for survival. This hypothesis was tested at Langwarrin (50 km SE. of Melbourne), where the vegetation and soil type are similar to Ringwood, the area studied by Gleadow and Ashton (1981), but the invasion is less advanced.

In Victoria, *P. undulatum* grows on a wide range of soil types, from sandy podzols on the Mornington Peninsula to the silty Hallam loam in the eastern suburbs and krasnozems in the Dandenong Ranges. The root habit of adult trees of *P. undulatum* varies with soil type (Gleadow and Ashton 1981), similar to several other species (Weaver and Clements 1938). Because *P. undulatum* aggressively invades sites differing widely in soil structure and fertility, the seedlings may also have a flexible root habit. Once established, seedlings must survive insect attacks and browsing. The ability of seedlings to recover from defoliation was tested in the glasshouse.

## Methods

### *Germination Tests*

#### *Temperature effects*

Duplicate samples of 30 fresh seeds collected from Ringwood were germinated on moistened filter paper (Whatman no. 30) in petri dishes at 4, 11, 16, 20 and 25°C. Previous experiments had shown that no germination occurred at 30°C. All germination tests were conducted in the dark as light significantly inhibits germination ( $X^2 = 16.54$ ;  $P < 0.01$ ). Germination was said to have occurred if the radicle had emerged more than 2 mm from the testa. The number of seeds which germinated after 60 d was recorded and expressed as a percentage of the total number of viable seeds. The viability of the ungerminated seeds was determined by cutting them and observing the condition of the embryo: if the embryo was soft and grey or the testa was empty the seed was declared inviable (Grose and Zimmer 1958; MacKay 1974). An analysis of variance was performed on arcsine-transformed data.

#### *Effects of storage conditions on viability*

Samples of seed were stored at different humidities. In a preliminary experiment seeds were stored at 0.8% R.H., at room temperature, in a desiccator containing concentrated sulfuric acid (Wilson 1921). Viability was measured every 2 to 3 months

by germinating three replicates of 12 seeds at 20°C. This was initially recorded after 35 d and then later in the experiment, since desiccated seeds take longer to imbibe enough water to initiate radicle emergence (Heydecker 1974).

The main experiment was of a 2 × 4 factorial design. Relative humidities of 20, 40, 60 and 80% were obtained with different concentrations of sulfuric acid (Wilson 1921). The desiccators were stored at 4 and 20°C, in the dark. The concentration of sulfuric acid was adjusted according to temperature to ensure that the humidities at the two temperatures were the same. The water potential ( $\psi$ , bars) of the air in each desiccator was calculated by the following formula (Salisbury and Ross 1969, p. 66):

$$\psi = 10 \cdot 7 T \log_{10}(100/H),$$

where  $T$  is the temperature (K) and  $H$  is the relative humidity. Samples of seed were removed at intervals for 16 months and two replicates of 30 seeds germinated at 20°C. An analysis of variance was performed on arcsine-transformed data. The moisture contents (wet wt basis) of duplicate samples of seed were measured three times in each of the storage experiments by drying the seed for 24 h at 100°C (Harrington 1973; Roberts 1974).

#### *Effect of animals on germination*

A captured silvereye was fed *P. undulatum* seeds to ensure collection of freshly defecated seed; 35 seeds were collected from the droppings and tested for germination at 20°C. The germinability of *P. undulatum* seeds found in fresh blackbird droppings was also tested. Droppings of the common ringtail possum from under a *P. undulatum* tree were dissected but only a few empty testas, probably of *P. undulatum*, were found. The seeds collected from the birds were germinated with fresh *P. undulatum* seeds as a control. The percentage germination of viable seed and the seed viability were measured after 55 d.

#### *Seedling Growth Habit*

##### *Growth on different soil types*

Krasnozern soil was collected at The Patch in the Dandenong Ranges (approx. 5 m from *P. undulatum* trees) and Hallam loam was collected at Ringwood (Gleadow and Ashton 1981). Plants and forest litter were cleared away from the surface and the soil excavated to 10 cm in two positions at each site. The soil was sieved twice through a 0.5 cm mesh, put into plastic tubes (40 cm deep, 5 cm in diam.) and arranged in a randomized block design. The water status of the two soils was very different due to the differences in structure.

Seedlings germinated from fresh seed, as above, were transplanted into the tubes in August 1977 and grown in the glasshouse. During the hotter months the glasshouse was shaded with 70% shade cloth. The temperature ranged between 15.5 and 40.0°C with a mean maximum of 24.9°C ± 5.0 and a mean minimum of 16.9°C ± 2.0. Eleven replicates on both soils were harvested 7, 14, 20 and 27 weeks after transplanting. Extra plants were harvested and mounted on paper to study the developing root and shoot system. The mean relative growth rate ( $R$ ) was calculated by the formula:

$$R = (\ln W_2 - \ln W_1)/(t_2 - t_1),$$

where  $W$  is the total dry wt,  $t$  is the time, subscripts 1 and 2 refer to the initial and final measurements (Evans 1972).

### Seedling growth in the field

Height and leaf number of established seedlings and the germination or death of any seedlings were recorded monthly in five plots (2 m × 1 m) at Langwarrin. The plots were selected to illustrate the growth of *P. undulatum* seedlings of different ages under different natural conditions and included sandy and clay soils.

### Artificial establishment of seedlings in the field

*P. undulatum* seedlings germinated from fresh seed, as above, were grown in krasnozem in seed trays in the glasshouse for 1 month, then hardened off outside for 1 month (October 1977). At this stage the seedlings had their cotyledons and most had at least two leaves: they were transplanted into the soil at Langwarrin on 5 November 1977. The experiment was of a split plot design. There were three major treatments: seedlings were planted into sites with no canopy (to be referred to as 'open'), at the base of mature eucalypts, or under young *P. undulatum* trees. Three replicates were planted at eight randomly selected subsites (24 seedlings per treatment). The seedlings were watered twice weekly with about 200 ml water each for 1 week and then once a week for the next 2 weeks. The number of surviving seedlings was recorded at regular intervals for the next 16 months.

**Table 1. Light conditions under three types of canopy at Langwarrin expressed as percentage of direct sunlight at the equinox and summer and winter solstices, and the percentage of diffuse sunlight**

Open, canopy with no overstorey; Euc, at the butt of a eucalypt; Pu, underneath a canopy of *P. undulatum*

Type of sunlight	Percentage of direct sunlight for canopy:		
	Open	Euc	Pu
Direct sun			
Summer	52.9 <sup>a</sup>	40.0 <sup>ab</sup>	25.5 <sup>b</sup>
Equinox	33.8 <sup>a</sup>	32.1 <sup>a</sup>	19.7 <sup>a</sup>
Winter	23.3 <sup>a</sup>	12.9 <sup>a</sup>	8.8 <sup>a</sup>
I.s.d. = 15.2*			
Diffuse light	44.3 <sup>a</sup>	38.0 <sup>ab</sup>	24.6 <sup>b</sup>
F = 15.6*			

\* $P < 0.05$ .

ab, Means in the same row with the same superscript are not significantly different at  $P < 0.05$  using l.s.d. for the direct sunlight and Duncan's multi-range tests (MRT) for the diffuse sunlight.

Light conditions were measured by hemispherical photography of the canopy (Anderson 1964) at two open, two eucalypt and two *P. undulatum* sites. The maximum direct sunlight possible at different times of the year was estimated by the line intercept method of Evans and Coombe (1959), and the results are summarized in Table 1. The light intensity of the diffuse sunlight under a dense *Cupressus macrocarpa* canopy, where *P. undulatum* is known to grow, was 11.6% and not significantly different from the *P. undulatum* canopy (Gleadow 1980).

Soil moisture of the A (0–5 cm) and B (5–10 cm) horizons at several sites was measured gravimetrically in February when it was dry and again in April 1978 after heavy rain (Table 2). Temperature and rainfall data for the experimental period, recorded at the Frankston Vegetable Research Station near Langwarrin, are presented (Fig. 1).

*Recovery from decapitation*

Seedlings of *P. undulatum*, germinated in the usual way, were transplanted into pots (12.5 cm in diam.) and grown under glasshouse conditions similar to those above for

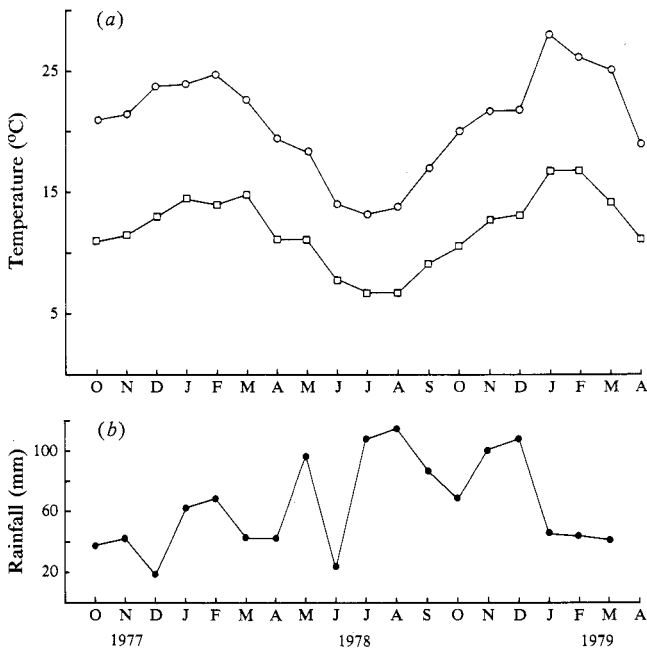
**Table 2.** Moisture content (%) of soils collected from the A(0–5 cm) and B(5–10 cm) horizons at three sites at Langwarrin in February and April 1978  
Abbreviations as for Table 1

	Soil moisture content (%) at site:			d.f.	F ratio
	Open	Euc	Pu		
February 1978					
A	18.2 <sup>a</sup>	26.9 <sup>b</sup>	19.0 <sup>a</sup>	45	11.63***
B	10.3 <sup>a</sup>	11.9 <sup>a</sup>	11.5 <sup>a</sup>	45	2.23n.s.
April 1978					
A	11.6 <sup>a</sup>	19.7 <sup>a</sup>	17.0 <sup>a</sup>	27	3.08n.s.
B	8.8 <sup>a</sup>	13.9 <sup>b</sup>	10.2 <sup>a</sup>	27	4.96*

\* $P < 0.05$ . \*\*\* $P < 0.001$ . n.s., Not significant.

Means in the same row with the same superscript are not significantly different at  $P < 0.05$  using Duncan's MRT.

10 months. Plants had just completed their first flush of growth from a vegetative bud when the shoots of seven individuals were removed to 3.0–4.5 cm from the soil



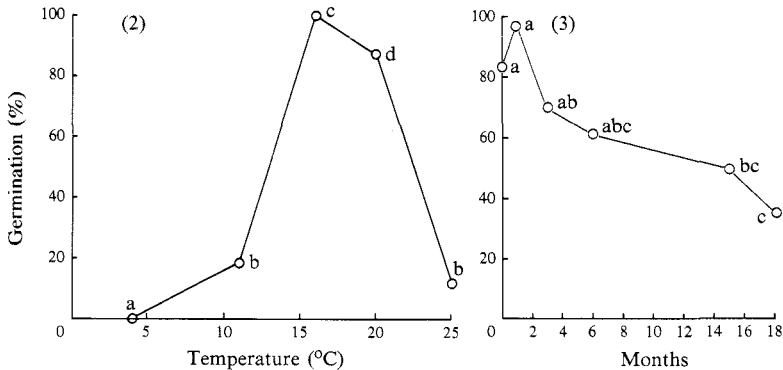
**Fig. 1.** (a) Mean monthly temperatures and (b) total monthly rainfall recorded near Langwarrin, Vic. from October 1977 to March 1979.

surface, leaving two to six leaves on each plant. Control plants were left intact. The height and leaf number of experimental plants were recorded for 8 months when the plants were harvested.

## Results and Discussion

### Germination Tests

The percentage germination was optimal between 18 and 21 °C: germination did not occur at 4 and 30 °C (Fig. 2). The incubation temperature affected the duration of the initial period before germination started. Seeds kept at 16 and 20 °C started to germinate after 35 d whereas those kept at lower and higher temperatures did not start until after 50 d.



**Fig. 2.** The effect of temperature on the germination of *P. undulatum* seeds. Coordinates with the same superscript letter are not significantly different at  $P < 0.05$  using Duncan's MRT.

**Fig. 3.** The percentage decrease in germinability of *P. undulatum* stored at 0.8% R.H. over time. Coordinates with the same superscript letter are not significantly different at  $P < 0.05$  using Duncan's MRT.

The total germination percentage of seed stored at 0.8% R.H. did not drop significantly until after 6 months' storage, and not again until 18 months when the germination dropped to 36.2% (Fig. 3). The percentage moisture content of the seed was between 1.4 and 30 during the first 6 months, as shown in the following tabulation.

Time:	0	2 days	2 weeks	3 months	6 months	<i>F</i> ratio
	29.7 <sup>a</sup>	10.2 <sup>ab</sup>	2.8 <sup>bc</sup>	4.8 <sup>bc</sup>	1.39 <sup>c</sup>	52.45**

Means with the same superscript are not significantly different at  $P < 0.05$  using Duncan's multi-range test (MRT) and the *F* ratio is significant at  $P < 0.01$ . As the moisture content usually reaches equilibrium with a constant R.H. within 2 to 3 weeks (Roberts 1960), it was assumed that the moisture content remained between 1.4 and 5% for the duration of the experiment.

There was no significant difference in the viability of seed stored at the range of humidities and two temperatures at any one time (Tables 3), although the viability did drop from nearly 100% to about 80% over the 16 months. High moisture content and temperatures have frequently been found to decrease longevity (e.g. Christensen 1974; Abdelmagid and Osman 1975). My results do not support this suggestion, as seed viability was maintained despite differences in the moisture content of the seeds (Fig. 4, cf. Table 3).

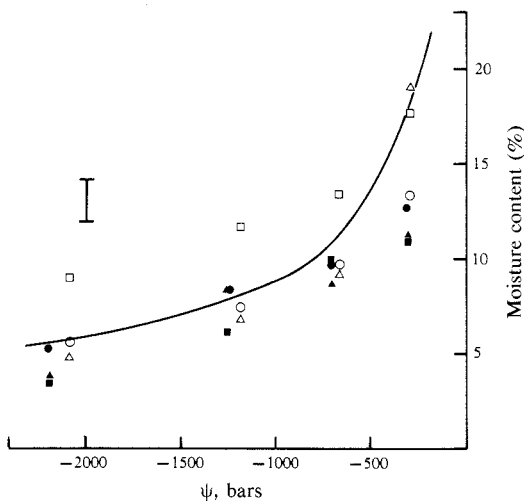
The germination of *P. undulatum* seed was unaffected after passing through the digestive tract of a silvereeye or a blackbird, as shown by the percentage viability (*v*) and germinability (*g*) in the following tabulation.

	Control	Silvereeye	Blackbird	$\chi^2$
<i>v</i>	100	100	100	
<i>g</i>	80	82	91	2.67 n.s.

**Table 3.** Mean percentage viability of *P. undulatum* seed stored at two temperatures and four relative humidities, and equivalent water potentials measured at intervals over 16 months  
l.s.d. = 9.64 at  $P < 0.05$

Months of storage	Mean percentage viability of seed at:							
	4°C				20°C			
	R.H.: 20 $\psi$ bars: 2072	40 1179	60 657	80% 287	R.H.: 20 $\psi$ bars: 2191	40 1248	60 695	80% 304
1	95.0	91.7	98.3	98.3	100.0	100.0	95.0	96.6
2	93.3	95.0	98.3	95.0	90.0	98.3	100.0	93.3
4	90.0	95.0	98.3	95.0	90.0	96.6	95.0	93.3
7	86.7	93.3	93.3	96.7	88.3	100.0	83.3	86.7
12	86.7	91.7	86.7	81.7	86.7	69.8	83.3	93.3
16	78.3	81.7	83.3	98.3	78.3	93.3	83.3	86.5

Cooper (1959) also obtained better than 90% germination from *P. undulatum* seed in blackbird droppings, and D. H. Ashton (personal communication) obtained high germination of seed collected from the gut of blackbirds which did not differ



**Fig. 4.** Moisture content of *P. undulatum* seeds stored at various water potentials for  $\circ$  2,  $\Delta$  7 and  $\square$  16 months at 4°C (open symbols) and 20°C (closed symbols).

significantly from the control. However, the silvereeye would only eat the seed if no other food was available and, similar to Gannon's (1935) observations, it tended to lick the sticky mucus from the seeds rather than to ingest them. Therefore, it is concluded that both these birds are capable of spreading *P. undulatum* but blackbirds are the main dispersal vector.

### Seedling Growth Habit

#### Seedling morphology

The first 2 or 3 alternate leaves are three-toothed and constitute a juvenile stage (Fig. 5). The next 8–10 leaves are entire, elliptic and increase in size with the developmental stage of the seedling (Fig. 6). This transitional stage continues for about 6 months in

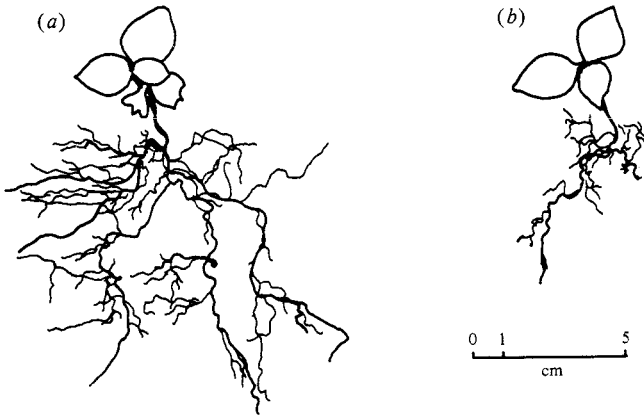


Fig. 5. The 14-week-old *P. undulatum* seedlings grown on (a) krasnozem and (b) Hallam loam in the glasshouse.

the glasshouse and over a year in the field, when the seedlings are about 11 cm tall (Table 4). At this stage a terminal vegetative bud forms at the stem apex and thereafter the pattern of growth completely changes. Five to ten leaves are initiated within one bud. On bud burst the stem rapidly elongates and the branch ends with a compact,

Table 4. Height of six representative seedlings measured from January 1978 to 1979 at Langwarrin

		Seedling height (cm)						
		1978					1979	
Jan.	Feb.	Apr.	May	July	Oct.	Dec.	Jan.	
3.8	5.6	6.0	6.0	6.2	7.3	7.7	7.7 <sup>A</sup>	
5.4	8.1	8.4	9.4	9.8	10.7	12.7	13.8 <sup>A</sup>	
9.5	10.9	11.4	11.8	11.6	11.6	13.2 <sup>B</sup>	14.0	
11.1	12.3	11.0	11.2	11.6	14.3 <sup>B</sup>	15.1	21.0 <sup>B</sup>	
15.6	16.3	16.5	18.7 <sup>B</sup>	19.1	19.9	26.4 <sup>B</sup>	24.5	
49.2 <sup>B</sup>	52.3	56.5 <sup>B</sup>	60.8	62.0	65.3 <sup>B</sup>	69.9	69.0	

<sup>A</sup> Growth in these seedlings was by development of single leaves.

<sup>B</sup> Height increase was a result of vegetative bud burst and the production of between 7 and 20 new leaves per plant.

almost whorl-like alternation of leaves. Bud burst occurs several times a year in seedlings but usually only once or twice in adult trees (Gleadow and Ashton 1981). The largest seedling measured in the field (initially 45 cm) produced three flushes of leaves in a year, almost doubling its height (Table 4).

Most seedlings at Langwarrin emerged in late autumn with the early rains; however, some also emerged in spring when the temperatures started to rise after winter (Table 5; Fig. 7). Although during the 1978–79 summer more seedlings died than were replaced,



the total number of seedlings increased after 14 months' observation, suggesting that the density of *P. undulatum* at Langwarrin is increasing.

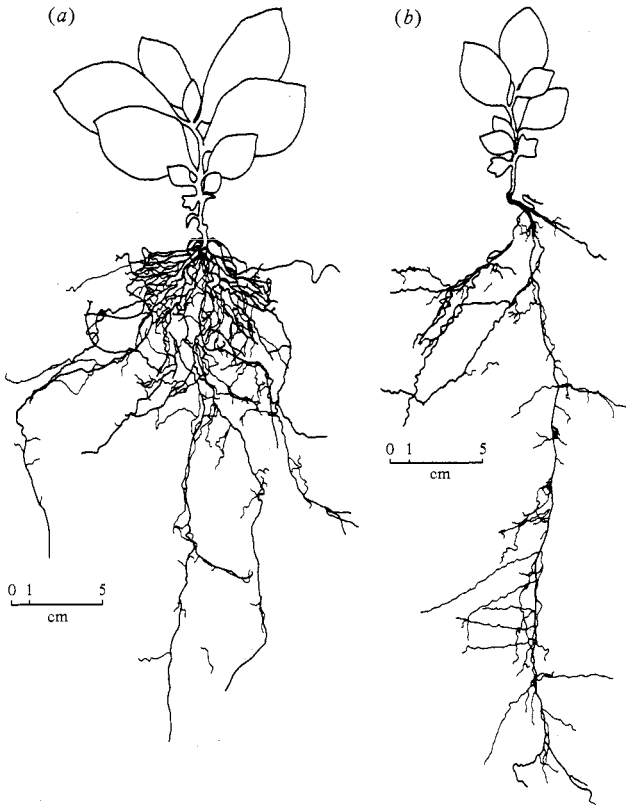


Fig. 6. The 20-week-old *P. undulatum* seedlings grown on (a) krasnozem and (b) Hallam loam in the glasshouse: at this stage there is a marked difference between the root systems.

Root habits of *P. undulatum* seedlings were different when grown in the two soil types after only 14 weeks of growth and the dichotomy was marked at 21 weeks. In the krasnozem soil the roots of the *P. undulatum* seedlings were diffuse and branched

Table 5. *F* ratios from the analysis of variance in total dry weight (*W*), height (*H*), root/shoot ratios (*R/S*) and relative growth rate (*R*) of *P. undulatum* seedlings grown on two soil types and harvested at four intervals

Treatment	d.f.	<i>W</i> <sup>A</sup>	<i>H</i>	<i>R/S</i>	<i>R</i>
Soil	1	7.09**	2.86n.s.	8.02**	3.03n.s.
Harvest	3	143.21***	29.56***	15.84***	4.20*
Soil × harvest	3	3.93*	1.80n.s.	9.33***	1.48n.s.
Error	70				

\**P* < 0.05. \*\**P* < 0.01. \*\*\**P* < 0.001. n.s., Not significant.

<sup>A</sup> Data log transformed prior to analysis.

whereas in the Hallam loam a definite tap-root developed (Figs 5 and 6), possibly along the path of least resistance since roots often behave in this way in compacted soils (Greacen *et al.* 1969). Seedlings of *P. undulatum* can thus adapt either to dry habitats with a tap-root or, with the diffuse root habit, to sites where the availability of moisture

and nutrients is high (Zimmer and Grose 1958). These two types of root habit have also been observed in adult trees (Gleadow and Ashton 1981).

Although the height and relative growth rates of seedlings grown on krasnozem and Hallam loam did not differ, the dry weight of the seedlings on the krasnozem was significantly greater (Fig. 8; Table 5). The root/shoot ratios of seedlings grown on both soil types were small (Fig. 8); in comparison, the root/shoot ratio at 10 weeks was 10 times smaller than that of *Eucalyptus obliqua* and *Acacia pycnantha* grown under similar conditions (Withers 1976). At about 20 weeks the root/shoot ratio increased markedly, although only temporarily, in seedlings grown on krasnozem; however, this was not observed in seedlings grown on Hallam loam. As a dormant, terminal bud developed between the third and fourth harvests, no height growth occurred in this interval (Fig. 8).

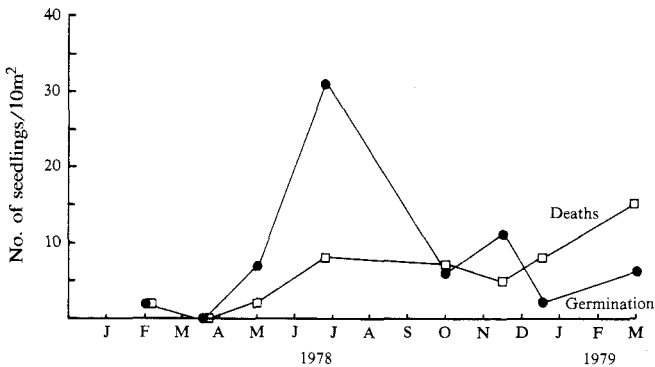


Fig. 7. The number of ● newly emerged seedlings in the permanent plots at Langwarrin measured at intervals over 15 months, and the number of □ those seedlings absent at subsequent measurements.

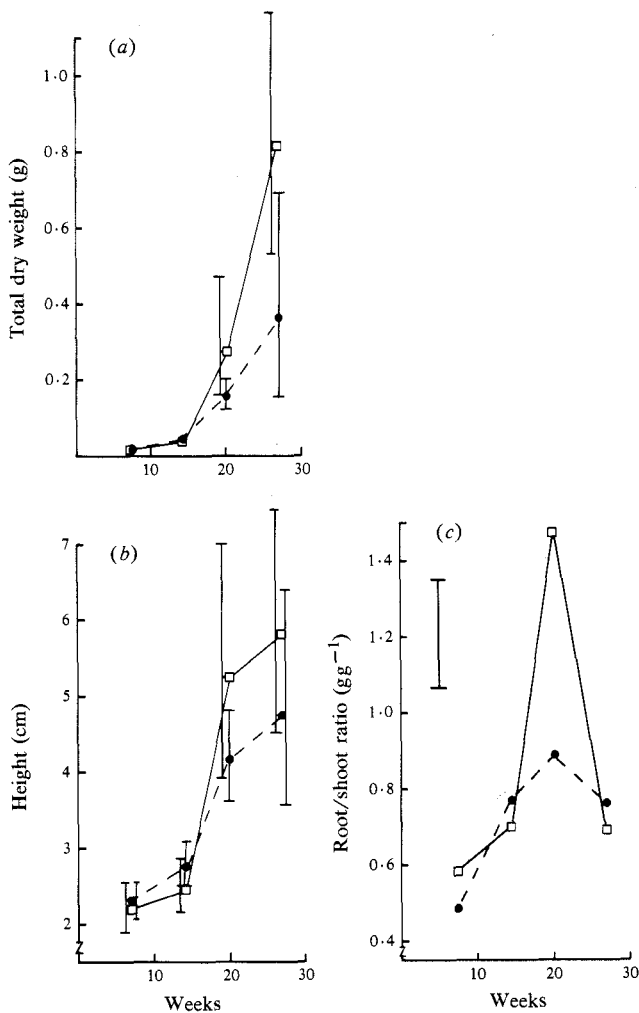
#### *Establishment of seedlings*

The survival of seedlings transplanted to Langwarrin was similar in all sites when they were watered. However, after watering was stopped there was a marked difference: most seedlings planted in the open died within 8 weeks while two-thirds of those under the *P. undulatum* trees were still alive after 1 year (Fig. 9). Survival at the eucalypt site was not much greater than at the open site. Differences in soil moisture content between the open and the *P. undulatum* sites do not explain these results (Table 2). The eucalypt sites were significantly wetter in both February and April, probably due to trunk flow. Light conditions appeared to be much more important: only shaded seedlings survived (Fig. 9). Although the light intensity at the eucalypt sites was not significantly different from that under the *P. undulatum* canopy (Table 1), this probably reflects the small sample size: at Ringwood, large numbers of seedlings of *P. undulatum* were found under canopies of *P. undulatum* where the light intensity was between 4 and 8% full sunlight (measured with a selenium cell). The low survival of seedlings at the eucalypt sites could also be due to allelopathy, as some eucalypts inhibit the growth of understorey species (del Moral *et al.* 1978). The difficulty of the first pioneering individuals becoming established in new areas emphasizes the necessity for *P. undulatum* to form a regeneration niche.

#### *Recovery from decapitation*

In the glasshouse all the decapitated plants recovered (Fig. 10). Initially, vegetative buds developed in the axils of the remaining leaves and at the scars where leaves had

been removed, continuing in a ring around the stem at these levels. Most of the buds produced three small leaves about 5 mm long; however, nearly all of these died leaving only two or three surviving shoots on each plant, hence the regenerated plants were multistemmed. The leaves were typically the young elliptic leaves rather than the toothed type (Fig. 5) and were produced one by one until the plants regained their initial height. After about 5 months a terminal bud developed.

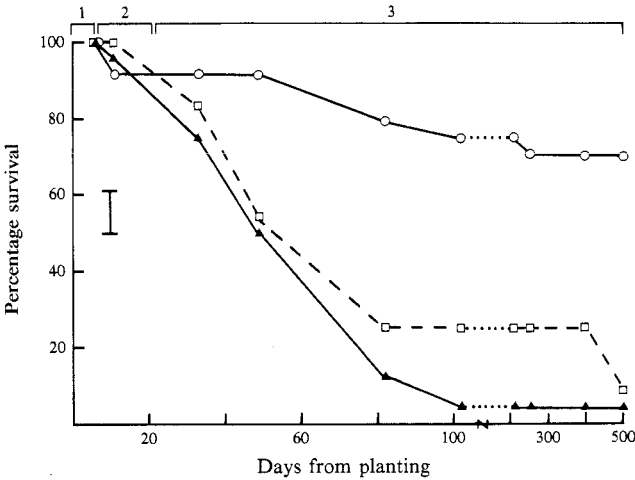


**Fig. 8.** (a) Total dry weight, (b) height and (c) root/shoot ratio of seedlings of *P. undulatum* grown on  $\square$  krasnozem and  $\bullet$  Hallam loam. Error bars represent  $t \times \text{s.e.}$  in (a) and (b), and in (c) was calculated using Scheffe's test ( $P < 0.05$ ).

The growth rate of the decapitated seedlings was not significantly greater than that of the control seedlings and the control plants remained taller (Fig. 10). The ability of the seedlings to recover suggests that if the shoots were damaged the seedlings would be able to survive. Several seedlings at Langwarrin that were partially defoliated by insects recovered, and preliminary observations of a *P. undulatum* tree scorched by a control burn at Langwarrin confirm that the shoots are able to resprout after low-temperature fires.

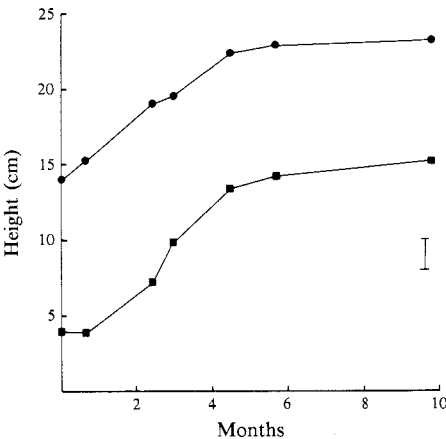
**General Discussion**

Blackbirds are the most likely vector of dispersal of *P. undulatum* in the Melbourne area. The expansion in the distribution of blackbirds parallels the invasion of *P. undulatum* into new areas. Although the seed is also viable after passing through the gut



**Fig. 9.** The percentage survival of *P. undulatum* seedlings planted ○ under a canopy of *P. undulatum*, □ next to a eucalypt trunk and ▲ in sites without a canopy at Langwarrin. Error bar represents the l.s.d. at  $P < 0.05$ . Nos 1, 2, 3 indicate twice weekly watering, once weekly watering and no artificial watering respectively.

of silvereyes, these birds prefer to eat other foods. Blackbirds tend to defecate while perching (P. Dann, personal communication) and they usually roost near the main trunk of a tree. This correlates with the preferential clumping of seedlings near the butts of established trees and implies that this pattern is the result of the uneven dispersal of the seed.



**Fig. 10.** Height of *P. undulatum* seedlings that were ■ decapitated or ● left intact. Error bar, calculated using Scheffe's test, represents the minimum significant difference between means at  $P < 0.05$ .

Although some seeds may germinate immediately after seed fall in spring (Ewart 1930), most do not do so until the following autumn (Fig. 6). The seed is probably unable to germinate in summer because of the high ambient temperatures and low humidities, dormancy being conditional (Fig. 2; Vegis 1964). The radicle takes at least 30 days to emerge from the testa, thus high humidities must be sustained for over 30 days for successful germination, compared with 2 days for lettuce seed (Brian *et al.* 1964).

After 16 months' storage, at moderate humidities and two temperatures, 80% of the seed was still viable. This suggests that seed falling in spring in the field could germinate the following year, given suitable conditions. On the other hand, dried seed does not keep well (Ewart 1930). The viability of seed stored for 18 months at 0.8% R.H. dropped by two-thirds (Fig. 3). If seed were deposited in sites lacking a canopy in the field, the hot sun probably would significantly reduce its viability and consequently reinforce the pattern of invasion initially dictated by seed dispersal. *P. undulatum* leaf litter, which reaches its peak fall about 2 months after the seed matures (Gleadow and Ashton 1981), may protect the seed on the ground from drying out and thus encourage seedlings to become established under the canopy of older *P. undulatum* trees. However, the results of other experiments (Gleadow 1980) suggest that if the seeds are buried deeper than 4 cm the seedlings are unable to emerge.

The total dry weight of seedlings grown on two different soil types was not severely reduced on the poorer soil (Fig. 8), reflecting the plasticity of both seedling and adult root systems (Gleadow and Ashton 1981). This result is consistent with the wide distribution of this species.

The survival of *P. undulatum* seedlings correlated with the light conditions rather than the soil moisture at each site (Fig. 9; Tables 1 and 2). The high temperatures and light intensities during the summer months were probably fatal to the young, juvenile seedlings growing in the sites lacking a canopy and, to a lesser extent, in the eucalypt sites. Both high temperatures and light intensities reduce the drought tolerance of *P. undulatum* seedlings (Gleadow 1980). The soil under the *P. undulatum* bushes was not significantly wetter than soil in the open sites, but the litter beneath the *P. undulatum* may provide nutrients for the seedlings and reduce the number of potential competitors (Gleadow and Ashton 1981). The differential survival of *P. undulatum* seedlings confirms the patchy pattern of invasion; however, it also emphasizes how difficult it is for the first invading seedlings to become established. It is essential, therefore, that *P. undulatum* forms a regeneration niche (Grubb 1977) under its own canopy in order to ensure the survival of succeeding generations. The capacity of *P. undulatum* to invade forests and establish such a niche suggests that the current changes in the Victorian vegetation are likely to be long lasting, provided that fire is excluded.

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