

Growth of *Pinus elliottii*, *P. pinaster* and *P. radiata* on coastal dune soils near Jervis Bay, Australian Capital Territory

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Summary

The growth of *Pinus elliottii*, *P. pinaster* and *P. radiata* on coastal dune soils is compared over a period of 23 y. Small growth responses to the application of urea, gypsum combined with potassium sulphate, dicalcium phosphate, and lime were obtained in the early phase of the experiment but they had dissipated at 15 y when the experiment was thinned. Immediately prior to thinning, stand basal area was 44.3, 33.9 and 39.4 m² ha⁻¹ for *P. radiata*, *P. pinaster* and *P. elliottii* respectively. In the second (late) phase of the experiment no growth response was obtained to super-phosphate applied with or without urea to thinned or non-thinned stands. In non-thinned stands, *P. radiata* and *P. elliottii* had similar growth rates; both species grew faster than *P. pinaster*. Thinning reduced productivity of *P. elliottii*. The results are discussed in relation to the notion of Type 1 and Type 2 growth responses, problems in forecasting future growth from early measurements, and the problem of estimating changes in stand productivity between rotations.

Keywords: forest management; growth models; increment; thinning; nutrition; fertilizers; *Pinus elliottii*; *Pinus pinaster*; *Pinus radiata*

Introduction

During the establishment and development of a plantation enterprise, the types of information needed by plantation managers, and thus research objectives, also evolve. Experiments that can efficiently cater for these changing needs are of particular value.

For example, pine plantations were established for the first time in 1956 on coastal sands at Jervis Bay, Australian Capital Territory. Early research sought to determine the most appropriate species and establishment methods for local conditions. Later — in the 1970s — the potential for boosting stand growth by applying fertiliser to established stands, particularly at the time of thinning, was explored.

This experimental material is now relevant to the worldwide interest in the sustainability of plantation enterprises. Changes in the productive capacity of plantations between successive rotations, particularly at management unit level, that can be attributed to changes in soil or other site characteristics (Smith *et al.* 2001), are of special significance. Such changes need to be distinguished

from changes in productivity that might arise from the use of different genetic stock and/or silvicultural practices.

To make good silvicultural decisions, plantation managers need to be able to assess the potential for various treatments to enhance or maintain productivity, and to estimate the various costs and likely benefits, sometimes over successive rotations. For decisions to be sound, they need to be firmly based on conceptual models that describe the expected effects of potential treatments on the pattern of plantation growth.

For categorizing distinctly different patterns of response to silvicultural treatment, Snowdon and Waring (1984) and Snowdon (2002) introduced the concept of Type 1 and Type 2 responses. A Type 1 response advances stand development through a phase of rapid early growth, but does not affect peak productivity as expressed, for example, through volume increment at its culmination. Once the growth rate ceases to be directly affected by the treatment, treated and non-treated stands follow parallel growth trajectories with a constant separation in time. A weed control treatment typically results in a positive Type 1 response compared to a treatment lacking weed control. Alternatively, poorer growth due to failure to control weeds could be considered a negative Type 1 response compared to that observed if weeds are controlled.

Type 2 responses also advance the stage of stand development, but are characterised by real and sustained changes in site productivity that affect peak productivity. They are usually associated with ameliorative treatments such as the addition of phosphorus fertiliser to some P-deficient soils. Conversely, loss of productivity between rotations can be interpreted as a negative Type 2 response.

The time course of volume increment in hypothetical stands that exhibit Type 1 and Type 2 responses is illustrated in Figure 1(a), and the consequences for volume yield are shown in Figure 1(b). The corresponding behaviour of basal area increment and basal area yield are illustrated in Figures 1(c) and 1(d) respectively.

A key question is whether different patterns of growth brought about by changes in genetic characteristics of stock (species, provenances, improved breeding lines) should be interpreted as Type 1 or as Type 2 responses. This information is crucial in choosing the correct model for projecting early growth

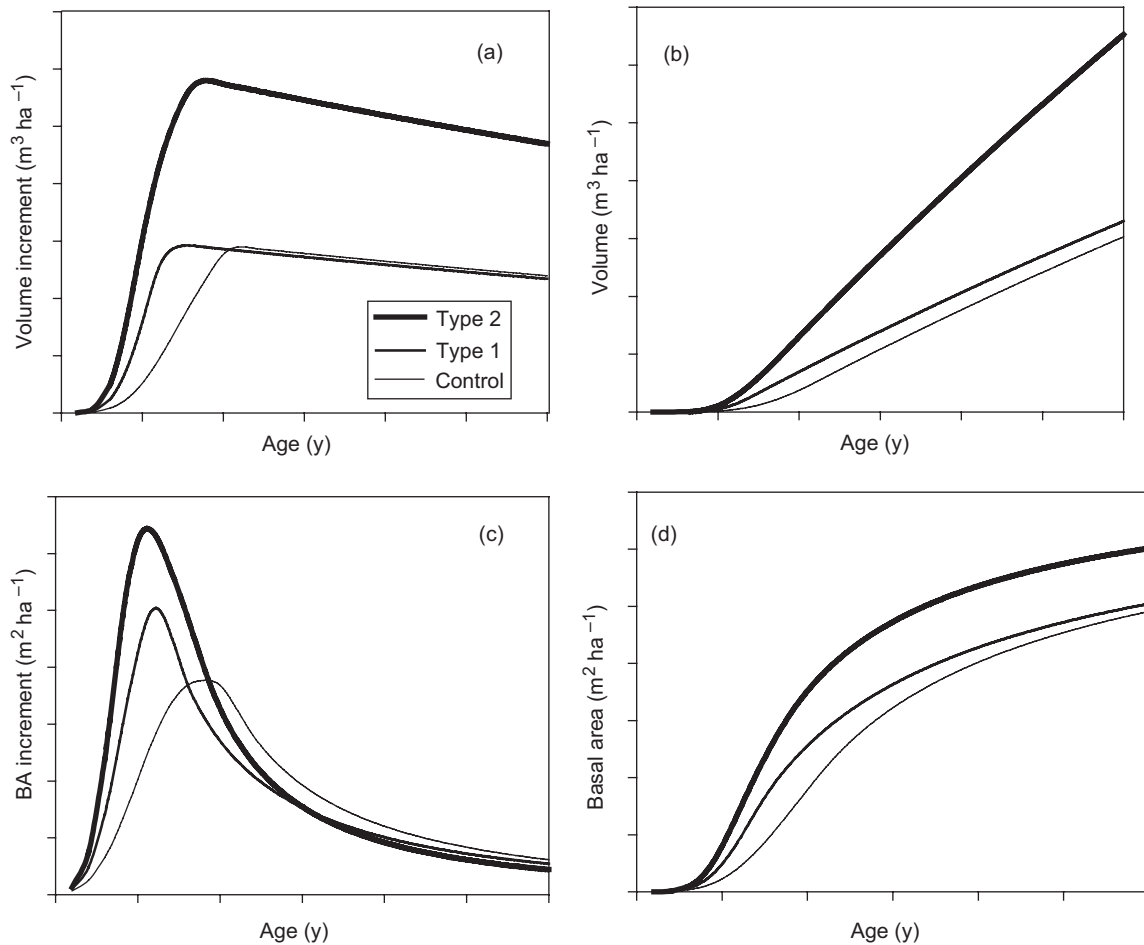


Figure 1. Type 1 and Type 2 responses to silvicultural treatments show distinctive patterns in (a) volume increment, (b) volume yield, (c) basal area increment, and (d) basal area yield. From Snowdon (2002).

measurements to make accurate estimates of future production. Since genetically improved stock is used to establish new rotations, it is particularly important to know whether a change in genotype, particularly that achieved by tree breeding, elicits a Type 2 response. If this is not the case, then a change in productivity between rotations could be attributed to a Type 2 response due to changes in site properties. Skinner *et al.* (1999) concluded from glasshouse and short-term field trials that genetically improved *P. radiata* seedlings were no more responsive to changes in soil conditions than unimproved stock. In older trees, however, the effects of genetic improvement on productivity are well established. In forest growth models a growth rate multiplier is often used to represent genetic improvement (e.g. Rehfeldt *et al.* 1991; Carson *et al.* 1999). This approach assumes that genetic improvement elicits a Type 2 response. There is some mensurational evidence that tree improvement can lead to Type 2 responses in New Zealand, but the results are inconsistent across sites (R.C. Woollons, University of Canterbury, *pers. comm.*).

This paper reports an experiment that was first designed to test the effects of various fertilisers on establishment and early growth of three pine species. It was modified at 15 y to test the effects of fertiliser in thinned and non-thinned stands. It is now re-examined to determine whether differences in growth between species can be best described as Type 1 or Type 2 responses.

Methods

Site description

Jervis Bay (35°10'S, 150°40'E) has an average annual rainfall of 1148 mm with 135 wet days per year and slight winter maximum. The climate is mild with an average maximum temperature in January of 23.8°C, and an average minimum in July of 9.2°C. The experimental site is about 2 km from the current ocean shoreline and consists of fixed sand dunes of variable depth over a sandstone basement. The native vegetation was sclerophyll forest dominated by *Eucalyptus pilularis* Sm. up to 30 m high in protected corridors, and 20 m on exposed dune crests. After clearing, logging slash was left in situ without burning. There was little live understorey at this time because the area had been burnt by wildfire shortly before the eucalypt forest was clearfelled.

The soils of the experimental site are podzols and groundwater podzols. A typical profile at mid-altitude shows grey surface sand grading to a bleached A2 horizon at 45 cm and a B horizon (at 60–120 cm) of yellowish-brown sand stained and sometimes weakly cemented by iron and organic matter. Below this is light yellow sand parent material to considerable depth. The surface soil consists of 91.5% coarse sand and 2% fine sand. It has a pH (1:1) of 4.80, 0.05% total soil nitrogen, 50 mg g⁻¹ total soil phosphorus, and a cation exchange capacity of 3–7 mmol(+) 100 g⁻¹.

Table 1. Fertiliser combinations used in Phase 1 and thinning x fertiliser combinations used in Phase 2 of pine species trial at Jervis Bay, ACT

Treatment	Phase 1					Phase 2	
	Rock phosphate (kg P ha ⁻¹)	Gypsum plus potassium chloride	Nitrogen as urea	Dicalcium phosphate	Lime	Thinning	Fertiliser
1	0					Thinned	
2	14					Thinned	P
3	35					Thinned	P
4	77					Thinned	NP
5	77	Yes					NP
6	77		Yes			Thinned	
7	77	Yes	Yes				
8	77		Yes	Yes			NP
9	77	Yes	Yes	Yes		Thinned	NP
10	77	Yes	Yes		Yes	Thinned	
11	77	Yes	Yes	Yes	Yes		

Experimental details — Phase 1

The first phase of the experiment tested growth responses by *P. elliotii*, *P. pinaster* and *P. radiata* to 11 treatments of various combinations of fertiliser (Table 1). The experimental site had an altitudinal range of about 10 m. The plots were stratified within four altitudinal strata. One replicate of *P. elliotii* was established within the lowest of the strata, typically in hollows between dunes. Another *P. elliotii* replicate was established in the highest, dune crest, stratum. The remaining two replicates of each of the three species were established within the two intermediate strata. Within these latter strata species were randomly assigned to plots. There were ten non-contiguous blocks of plots with each block containing from 2 to 19 plots. The plots were 18.3 m x 18.3 m, each containing 64 trees at a spacing of 2.3 m x 2.3 m. Areas between the plots were planted with *P. elliotii*. The experiment was planted during the winter of 1958.

The 11 fertiliser combinations (Table 1) were applied in four equal applications in autumn 1959, December 1959, October 1960 and August 1961. The total amounts of phosphorus supplied by three rates of rock phosphate were 14, 35 and 77 kg P ha⁻¹ respectively, while some treatments received supplementary dicalcium phosphate (23 kg P ha⁻¹). Lime was applied at 1620 kg ha⁻¹ to test whether this would reduce leaching losses of phosphorus. Gypsum (97 kg S ha⁻¹) and potassium chloride (113 kg K ha⁻¹) were applied in combination. Urea (73 kg N ha⁻¹) was used to supply nitrogen. Fertiliser was spread evenly over a circle, 1 m in diameter, centered on each tree. Competition was strong from indigenous grasses (*Imperata*), ferns (*Pteridium*), vines (*Hardenbergia*, *Kennedy*), shrubs (*Acacia*, *Banksia*, *Casuarina*) and regenerating *Eucalyptus* during the first 2 y, before being reduced in mid-1960 by manual slashing.

The central 16 trees in each plot were measured. Heights were measured at 1, 2, 3, 4 and 8 y after planting. Diameters at breast height were measured at 8, 12 and 15 y.

Experimental details — Phase 2

In 1970 the experiment was redesigned. Seven treatments were thinned (Table 1). A computer algorithm was used to select trees for thinning. On each pass of the algorithm a score was calculated for each tree based on the desirability of retaining that tree. This involved a field evaluation of stem form, tree size, and a measure of local stocking density based on the ratio of basal area of the target tree to the sum of basal areas of trees at eight surrounding planting positions (including those in adjacent plots). The algorithm was applied iteratively to plots within blocks of plots.

After scoring each tree within each plot, one tree was nominated for thinning in each plot within the block before returning to the first plot. Tree scores were recalculated taking into account trees already selected for thinning; then the next tree in each plot was chosen for thinning. This ensured that adjustments to thinning in a particular plot were made according to the thinning schedules in adjacent plots. In each plot both the central 16 measured trees and the entire plot were thinned as closely as possible to the nominated residual basal area for the species. These were based on then current Australian practice and were 20.7 m² ha⁻¹ for *P. radiata*, 17.4 m² ha⁻¹ for *P. pinaster*, and 16.1 m² ha⁻¹ for *P. elliotii*. However, while marked for thinning in 1970, the trees were not removed until early in 1973. Immediately prior to thinning stand basal area was 44.3, 33.9 and 39.4 m² ha⁻¹ for *P. radiata*, *P. pinaster* and *P. elliotii* respectively. Average basal area retained after thinning was 28.1 m² ha⁻¹ for *P. radiata*, 25.6 m² ha⁻¹ for *P. pinaster* and 22.5 m² ha⁻¹ for *P. elliotii*. Residual stockings were 840, 1160 and 805 stems ha⁻¹ for *P. radiata*, *P. pinaster* and *P. elliotii* respectively. At thinning there was negligible understorey. Samples from unthinned plots indicated that each species had accumulated 35 t ha⁻¹ of needle litter.

Phosphorus fertiliser (P) was applied to two of the seven thinned treatments, and NP fertiliser to two. Three thinned treatments received no additional fertiliser (Table 1). Two of the non-thinned treatments were treated with NP fertiliser. The P treatment was a

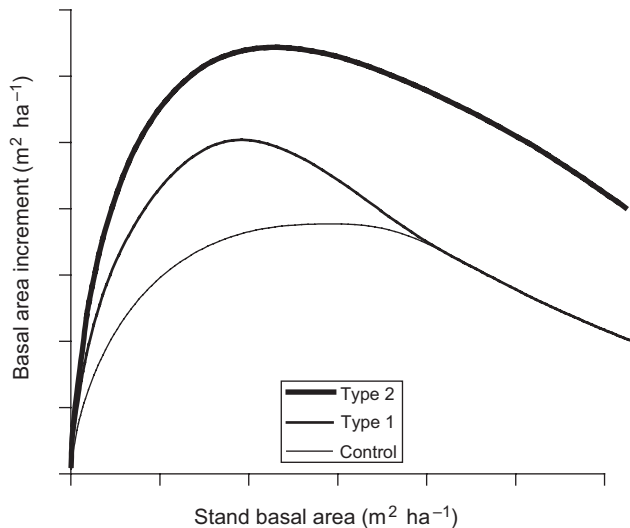


Figure 2. Development of basal area increment of Type 1 and Type 2 responses as a function of stand development as measured by stand basal area. From Snowdon (2002).

mixture of superphosphate (64 kg P ha⁻¹, 68 kg S ha⁻¹) and rock phosphate (60 kg P ha⁻¹). In the NP treatment these were supplemented with 284 kg ha⁻¹ urea (131 kg N ha⁻¹). The fertilisers were broadcast in early September 1973. A second application of superphosphate and urea was made in September 1974.

Diameters of all retained trees were measured at annual or biennial intervals until 1981. In 1979 the heights of remaining trees were measured in the central 16-tree Phase 1 measurement plot.

Data analysis — fertiliser and thinning effects

Response in Phase 1 of the study was assessed in terms of height growth to 8 y of age and basal area to 15 y. Analyses of covariance were carried out using initial seedling height and/or plot altitude as covariates. Orthogonal contrasts were used to separate the effects of individual fertilisers from the various treatment combinations.

Increments over the 8-y period following thinning (Phase 2) were used to assess basal area response, with particular emphasis on the effects of fertiliser applied at the time of thinning. Analyses of covariance were also used to adjust increments for differences in stand development prior to thinning. Because covariance analyses can be compromised in thinning trials (Woollons 1985; Snowdon and Woollons 1993), preliminary regression analyses were used to determine whether differences between species or thinning treatments affected the coefficient for the covariate. Where this occurred, separate analyses were made.

The nature of species growth patterns

It is inappropriate to use initial basal area or growth rates prior to thinning as covariates for testing the effects of species or thinning treatments on subsequent growth rate because the covariate is invariably confounded with the treatment. The approach taken here was to directly compare the growth curves. A quadratic function was fitted to the basal area measurements taken after

Table 2. Average height (m) of three *Pinus* species on coastal sand dunes at Jervis Bay, ACT

Age (y)	<i>P. elliottii</i>	<i>P. pinaster</i>	<i>P. radiata</i>	sed
0	0.22	0.28	0.52	0.014
1	0.28	0.32	0.52	0.022
2	0.63	0.45	0.91	0.050
3	1.08	0.69	1.59	0.106
4	1.74	1.20	2.76	0.179
8	6.08	5.56	10.25	0.432
21	17.0	16.7	20.0	0.471
Site index @ 21 y	18.9	19.6	23.9	0.418

sed = standard error of difference between means

thinning, and the coefficients were examined for significant effects of treatments (Snowdon and Woollons 1993; Woollons *et al.* 1994).

Type 1 and Type 2 responses to treatments applied during plantation establishment may be indistinguishable during the early growth period. Rather, they are distinguished by the extent to which the treatments enhance growth increment in later stages of plantation development (Fig. 1). Direct comparison of stand increment at a particular age can be misleading. It is not unusual for a stand to respond to some treatment during the rapid early growth phase, but to have a smaller increment than the control as stand increments decline with age (see Fig. 1(c)). This occurs because the stage of stand development of the treated stand is advanced with respect to the control stand. In Figure 2, basal area increment is plotted against stand basal area, used here as a measure of the stage of stand development. It is clear that the control stand did not have a greater increment at any stage of stand development than the stand exhibiting a Type 2 response. However, eventually the control stand will achieve the same increment as a stand with a Type 1 response. Ideally any comparison between growth curves should be made when there are similar conditions with respect to site occupancy; for example, as measured by some estimate of yield such as basal area. Such comparisons usually need to be made when the stands are at different ages.

Based on this argument, quadratic functions relating stand basal area to stand age were used to approximate the yield curves in the unthinned plots for the period 8–23 y of age. These equations were solved to estimate the age when 20 m² ha⁻¹ basal area was achieved. This arbitrary quantity was assumed to represent full basal area stocking for unthinned stands of all species. The differences in time taken by the three species to reach full stocking was regarded as an estimate of the degree of advancement in stand development due to a Type 1 or Type 2 response. Basal area increment for the 5-y period immediately after achieving full stocking was also estimated from the quadratic function. Provided a difference in the degree of advancement of stand development exists, similarity in increment indicates a Type 1 response has occurred while significant differences in increment indicate that a Type 2 response has occurred.

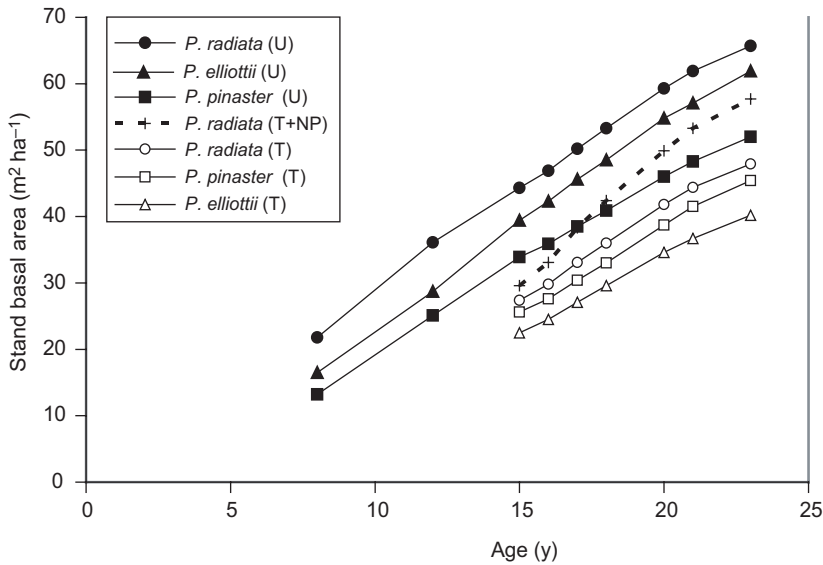


Figure 3. Growth of unthinned (U) and thinned (T) pines at Jervis Bay including the response of *P. radiata* to application of NP fertiliser

Results

Phase 1

Differences between the three species in mean height growth were highly significant ($P < 0.001$) throughout the trial (Table 2). By age 8 y, height of *P. elliotii* was 6.2 m within the intermediate strata, but 0.5 m better in dune hollows and 0.9 m poorer on dune crests. When testing effects of fertiliser application in data from the first three measurements after treatment, the height at age 1 y was used as a covariate. During the first growing season after fertiliser application, nitrogen increased height of all species by 6 cm ($P < 0.02$), while the combination of gypsum with potassium chloride further increased height by 5 cm ($P < 0.05$). There was no evidence of fertiliser response at any subsequent height measurement. By age 8 y, plot altitude had also become a significant covariate.

Differences between the three species in basal area growth were highly significant ($P < 0.001$) throughout both phases of the trial (Fig. 3). Plot altitude had a significant effect on growth of

Table 3. Responses to fertiliser application and thinning at age 15 y of stands of three pine species grown on coastal sand dunes at Jervis Bay, ACT. Data are adjusted basal area increments ($m^2 ha^{-1}$) during an 8-y period.

Species	Thinning	Fertiliser effects				Covariate coefficient
		Nil	P	NP	sed	
<i>P. elliotii</i>	Not thinned	23.1	–	21.9	1.34	1.95
<i>P. elliotii</i>	Thinned	18.0	17.0	17.8	1.37	0.88
<i>P. pinaster</i>	Not thinned	17.3	–	18.8	2.67	1.04
<i>P. pinaster</i>	Thinned	19.6	21.0	19.1	2.13	0.88
<i>P. radiata</i>	Not thinned	21.9	–	20.9	1.99	2.16
<i>P. radiata</i>	Thinned	22.3	23.4	22.6	1.60	2.17

sed = standard error of difference between means

P. elliotii. At age 8 y, the trees had produced $2.7 m^2 ha^{-1}$ more basal area in the dune hollows than in the intermediate strata ($17.0 m^2 ha^{-1}$) and $3.2 m^2 ha^{-1}$ less on dune crests. These differences widened with time.

When testing the response in basal area to fertiliser application, initial height and altitude were used as covariates. At age 8 y, application of dicalcium phosphate had increased basal area of all species by an average of $2.4 m^2 ha^{-1}$ ($P < 0.02$). Application of nitrogen increased basal area but reached statistical significance ($P < 0.05$) only with *P. pinaster* ($3.7 m^2 ha^{-1}$). By age 12 y, responses to nitrogen and phosphorus were no longer evident in any species, but application of lime had reduced basal area by an average of $3.1 m^2 ha^{-1}$ over all species. By age 15 y, there was no evidence of growth response to any of the original fertiliser treatments.

Phase 2

Basal area growth in the 8 y following thinning at age 15 y is illustrated in Figure 3. Preliminary analyses indicated that response to fertiliser applied at age 15 y occurred only when the NP combination was applied to thinned *P. radiata*. Subsequent analyses used basal area increment for the 3 y prior to re-treatment as a covariate for the increment during the next 8 y. Data for each species x thinning combination were analysed separately because regression coefficients varied between groups. There was no evidence of a response to fertiliser application in any species or thinning combination (Table 3). Closer examination of the data indicated that the stands of *P. radiata* destined to be thinned and fertilised with the NP combination had been growing significantly ($P < 0.01$) faster than comparable stands prior to treatment. Covariance analysis identified the spurious nature of the apparent response of *P. radiata* to NP fertiliser after thinning (Fig. 3). Thinning significantly reduced increment in *P. elliotii* but not in the other species.

Comparison of species' growth patterns

Basal area growth was very well modelled by quadratic functions. They accounted for more than 99.4% of variation within plots and had an average standard error for observations of $0.73 m^2 ha^{-1}$. Analyses of variance of model coefficients indicated that in unthinned stands there was no significant difference between the intercepts and linear coefficients for the growth curves of *P. elliotii* and *P. radiata* during the period 15–23 y of age, and the quadratic components were barely significantly different (Table 4). The coefficients for both species, however, were significantly different from those for *P. pinaster*, indicating that that species had a distinctly different growth pattern. As expected, thinning tended to have a marked effect on the intercepts. In *P. pinaster* and *P. radiata* there was little change in the linear and quadratic components, indicating that there was little change in growth rates after thinning. In contrast, there was a marked drop in the linear component for *P. elliotii*, indicating that thinning had reduced the rate of growth.

Table 4. Coefficients of quadratic equations, $y = a + bt + ct^2$, for three pine species grown under two thinning regimes on coastal sands at Jervis Bay, ACT, where y is basal area increment (m^2ha^{-1}) from 8 to 23 y of age and t is age in years

Thinning treatment and coefficient	<i>P. elliotii</i>	<i>P. pinaster</i>	<i>P. radiata</i>	sed
Unthinned stands				
a	-27.4	-12.6	-26.2	6.0
b	5.52	3.58	6.25	0.60
c	-0.070	-0.033	-0.092	0.008
Thinned stands				
a	-10.2	-17.9	-24.5*	5.9
b	4.20	3.71	6.07*	0.53
c	-0.051	-0.030	-0.090*	0.012

sed = standard error of difference between means

* = excluding stands treated with NP

Quadratic growth curves fitted to data from unthinned stands for the period 8–23 y of age were solved to estimate the time taken to reach full stocking, assumed here to be $20 \text{ m}^2\text{ha}^{-1}$ (Table 5). *Pinus radiata* reached full stocking significantly sooner than *P. elliotii* (1.7 y) and *P. pinaster* (2.9 y). Growth in stand basal area after achieving full stocking is illustrated in Figure 4. Five-year increments for *P. radiata* and *P. elliotii* were not significantly different, but both species grew significantly faster than *P. pinaster*. Thus, in terms of growth rate under full stocking, *P. radiata* and *P. elliotii* exhibit Type 2 responses relative to *P. pinaster*. In contrast, *P. radiata* exhibited a Type 1 response relative to *P. elliotii* by having a similar growth rate under full stocking, but a faster early growth rate.

Discussion

During the 23-y history of this trial, the information obtained from it has shifted to meet the changing needs of plantation managers and researchers. The broad conclusions from this trial are:

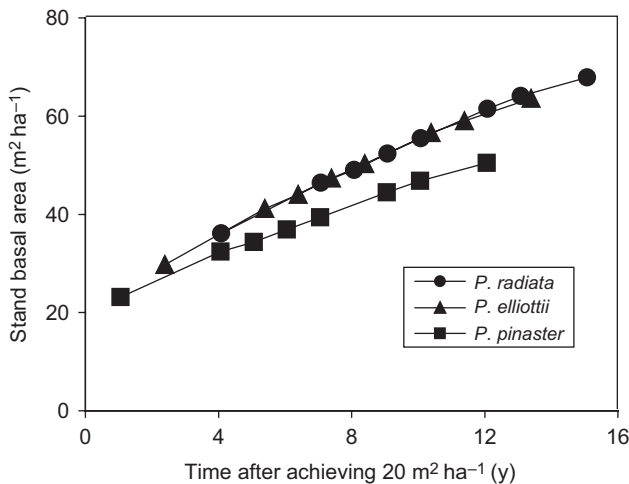


Figure 4. Basal area growth of unthinned stands after achieving a basal area of $20 \text{ m}^2\text{ha}^{-1}$. Faster growth of *P. radiata* and *P. elliotii* compared to *P. pinaster* indicates a Type 2 response.

Table 5. Estimated age for unthinned stands to achieve full stocking (a basal area of $20 \text{ m}^2\text{ha}^{-1}$) and subsequent 5-y basal area increment by three species of pine grown on coastal sands at Jervis Bay, ACT

	<i>P. elliotii</i>	<i>P. pinaster</i>	<i>P. radiata</i>	sed
Age at full stocking (y)	9.2	10.4	7.5	0.7
Five-year increment (m^2ha^{-1})	17.1	14.1	18.9	1.5

sed = standard error of difference between means

(1) appropriate experimental design, careful measurement and close attention to statistical analysis are essential for proper evaluation of growth responses; (2) responses to fertiliser application on dune sands of Jervis Bay are different from those obtained elsewhere; (3) differences in growth patterns between species indicate that both Type 1 and Type 2 responses can occur; (4) early response may not be a good basis for forecasting future yield; and (5) changes in productivity between rotations can be interpreted as a Type 2 response. Each of these is discussed below.

Experimental design, analysis and interpretation

It is unusual for genetic material to be tested in randomised field trials with plots sufficiently large to approximate stand conditions. For example, in a comparison of radiata pine seed-lots in New South Wales, only one of 14 trials was established with large plots (Johnson 1991): line plots containing four to ten trees were more common. Large plots are necessary to capture the effects of increasing competition for resources as stands develop, and to determine interactions with silvicultural treatments such as thinning.

Trials of genetic material are usually measured infrequently (D.J. Spencer, CSIRO Forestry and Forest Products, *pers. comm.*). Frequent measurements are required for mathematical description of growth curves and for assessing the nature of growth responses — for example, whether responses are Type 1 or Type 2. It is also important that the layout of plots with trees of different genetic origin be randomised so that advantage can be taken of the increased precision attainable with analyses of covariance. This is important where there are variations in site and stand properties such as plot environment or differences in initial growing stock.

Analyses of covariance become particularly important when operations such as thinning alter the physical nature of the experimental units (Woollons 1985; Woollons *et al.* 1994). It is important to note that in this and an earlier study of this experiment (Woollons and Whyte 1988, Trial No. 2), different types and numbers of covariates were required at different stages of stand growth, and according to the nature of the statistical tests being undertaken. Without this approach small growth responses to fertiliser application would not have been detected, and the nature of differences between species might have been misinterpreted.

Responses to fertiliser

The choice of fertilisers for Phase 1 of the field trial was based on the results of a glasshouse omission-type pot trial where each of

the species was grown in sand from the Jervis Bay area. In this trial, gross deficiencies of nitrogen and phosphorus developed in the first year of growth, followed by deficiency of sulphur in the second year and potassium in the third year (F&TB 1958). However, growth responses obtained in the subsequent field experiment were small and ephemeral. This can be partly attributed to the lack of early weed control. At that time it was considered that control of weeds by hand or mechanical slashing would be too expensive for normal plantation practice. Herbicides were not then regarded as an option. Subsequent trials showed that early control of competition from weeds could increase the volume of *P. elliotii* at 7 y by 16% (Waring 1968), and that application of N fertilisers in combination with competition control would result in improved growth of *P. elliotii* (F&TB 1962) and several *Eucalyptus* species (Snowdon 1991).

Despite the low concentrations of total phosphorus in the soil, about 10% was in a readily available form (Waring 1981). This, and ready exploitation of the soil volume by tree roots, may have contributed to the lack of any sustained responses to P fertiliser. Moreover, no responses to the application of P fertiliser were obtained in other trials in the area (F&TB 1962; Snowdon 1991). Similarly, no responses to the application of K fertilisers were obtained in any succeeding field trials. After comparing nutrient responses in pot and field trials on a range of soil types it has been concluded that the occurrence of S deficiency in pot trials was an artefact of the method.

In Australia, growth responses from the application of fertiliser in combination with thinning have been obtained under a wide range of conditions — from densely stocked field trials (11 960 stems ha⁻¹), 3–5 y after establishment (Snowdon and Waring 1995), to mature stands receiving their final thinning (Snowdon *et al.* 1995). Growth responses following fertiliser application to P-deficient stands are usual on most soils, even in the absence of thinning. For example, on deep coastal sands in Western Australia a 40% response in volume increment was obtained in 20-y-old *P. pinaster* (Butcher 1977). Responses to nitrogen may not be obtained unless any underlying deficiency of phosphorus is first corrected (Snowdon and Waring 1990). On sites of moderate to high fertility, or where P fertiliser has been added, growth responses by *P. radiata* to the application of N fertiliser at the time of thinning have commonly given a 20% increase in basal area or volume increment over the next 5 y (Snowdon 2002). Results such as these have also been obtained with *P. radiata* on deep sands in South Australia (Carlyle 1995).

Against this background the lack of response at Jervis Bay is unusual. Phosphorus concentrations in *P. elliotii* foliage from two other trials in the area were 0.11% P (F&TB 1966) and 0.12–0.20% P (Waring 1968) respectively, giving further indication that phosphorus supply was adequate. Corresponding foliar concentrations of nitrogen were in the range 0.90–1.18% N. This is probably adequate for normal growth (Simpson and Osborne 1993), but may be insufficient to cater for the extra nitrogen required for crown expansion after thinning. This demand is such that even on highly fertile sites growth responses can be obtained by applying nitrogenous fertilizers (Woollons and Will 1975; Woollons 1985).

It is likely that a substantial fraction of the N fertiliser was lost from the dune surface soil before it could be taken up by trees.

Large volatilisation losses are common when urea is used as a fertiliser. The litter would retain some of the ammonium ions released, but because the soils have a very low cation exchange capacity the ammonium would be rapidly leached from the system during heavy rainfall. There is some evidence that growth responses by *P. elliotii* can be obtained on Jervis Bay sands if less soluble forms of nitrogen fertiliser are applied. Experiments described by Waring (1968) were thinned at 7 and 8 y of age by removing 0, 25, 50 or 75% of the stems. At thinning, John Innes Base, an NPK fertiliser with N supplied from hoof and horn meal, was applied to half of the plots. The following year this was supplemented with ammonium phosphate. Twelve years later basal area increment on thinned plots was reduced by 13% for each 25% reduction in stocking. Response in basal area increment due to application of fertiliser was 11% after 2 y, but on only the two most heavily thinned treatments (Woollons 1988).

Growth patterns in different species

Pinus radiata had better height growth than the other species from the beginning but it is not known whether this was due to better planting stock or to an inherent difference between species. By age 8 y *P. radiata* had established a height advantage of >4 m over the other species, but by 21 y this had been partly eroded, demonstrating a typical Type 1 response. This result can be compared to dominant height growth of 10 provenances of *P. pinaster* on stabilised coastal dune soils in France (Danion 1994). At 10 y, nine of the provenances were in the height range 3.1–6.0 m. By 20 y the range had increased to 8.2–11.8 m. This height difference was maintained until the final measurement at 36 y when growth projections with a Lundquist–Mattern function suggested the differences would be maintained with little change in ranking and at similar magnitudes until 60 y. Early development of differences in height followed by a sustained period during which the differences are maintained is evidence for Type 1 responses among these nine provenances. However, the tenth and poorest provenance was 1.1 m shorter than the next best at 20 y, and 2.5 m shorter at 36 y. The increasing difference between these two provenances is characteristic of a negative Type 2 response of the tenth provenance with respect to the next best.

Basal area can be a better determinant of growth and response patterns than height because it is more closely representative of volume growth. The three species evaluated exhibited inherent differences in growth rate during the early years of plantation establishment, but later the expression of these differences was suppressed when stand and site factors became the dominant determinants of stand growth. At this later stage, that is, beyond full site occupancy, *P. radiata* and *P. elliotii* had similar growth rates indicative of a Type 1 response. Both species grew better than *P. pinaster* under full site occupancy. This indicates that relative to *P. pinaster* the other species exhibited Type 2 responses. Evidence from other trials is scanty. However, results with *P. radiata* grown on deep sands near Mt Gambier indicate that inbreeding depression can result in a negative (i.e. with respect to normal breeding stock) Type 2 response (Wu *et al.* 1998).

Genotypes vary in the way they respond to various limiting conditions for growth. Across a range of sites this can result in a marked genotype × environment interaction (Matheson and Raymond 1984). The concept of Type 1 and Type 2 responses can

be used to interpret this observation. Under plantation conditions, differences between genotypes are first expressed by their varying capacity to capture growing space through fast early growth. On highly fertile, well watered sites it is conceivable that the capacity for faster growth by some genotypes could continue to be expressed throughout the useful life of the plantation. This circumstance would be considered a Type 2 response and could be used to justify the use of simple multipliers in growth models to represent tree improvement (Carson *et al.* 1999). Under Australian conditions it is more usual for pine plantation growth to become constrained by the declining availability of water or nutrients as plantations mature. Although there may be differences between genotypes in the efficiency with which limited resources are used, these are probably small and difficult to measure in terms of stand growth. As a consequence the capacity for faster growth exhibited during plantation establishment is no longer expressed, so the differences in growth between genotypes can be characterised as a Type 1 responses.

Forecasting future growth

Early assessments of stand growth between 6 and 10 y after planting are commonly used to forecast future growth so that marketing prospects and other economic evaluations can be made. It is usually assumed that these early measurements can be used to estimate site index or site quality so that an existing model of stand growth can be used to forecast growth. No problems arise in the forecasts provided that the growth model has been calibrated with data collected from stands grown under the same silvicultural regime as the inventory data. Problems arise when the inventory data are derived from a silvicultural regime different from that used to calibrate the model.

The implication of the concepts of Type 1 and Type 2 responses is that the general shape of the growth curves have changed with changes in silviculture and/or tree breeding. Under Australian conditions, a conservative approach for forecasting future stand growth is to assume that in most cases no change in site occurs but that stand development has been brought forward so that the rotation age can be reduced, that is, a Type 1 response is most likely to have occurred. The reliability of yield forecasting would be greatly improved if it were based on at least two measurements, some years apart, and sufficiently delayed in time so that the two types of response could be distinguished by differences in volume increment after canopy closure. Similar precautions need to be taken when applying models to stands to which treatments have been applied at a later age.

With *P. radiata* there is evidence that, compared to 1960s silviculture, stand development can be advanced by about three years by Type 1 responses (Snowdon 2002). Forecasts based on the incorrect assumption that a Type 2 response has occurred will overestimate future production and will bias economic evaluations.

Comparing productivity across rotations

Change in the productive capacity of plantation sites between rotations is most likely to occur on soils of light texture with low organic matter content and with little capacity to retain major nutrients such as nitrogen and phosphorus. Change may also

occur on heavy-textured soils where the water-holding capacity can be reduced by soil compaction or loss of organic matter. Changes in productive capacity between rotations can be viewed as Type 2 responses. However, comparisons of productivity between rotations can be confused because of differences in stand establishment and tending practices, or changes in genetic material. If growth and yield data are used to infer changes in site resources, these additional factors must be accommodated. Type 2 growth responses can be distinguished from Type 1 responses by growth rates achieved under full stocking. However, change in growth rate cannot be ascribed to change in site resources unless other potential differences between rotations, for example in genetic stock, which could lead to Type 2 responses, have been eliminated from consideration.

The results obtained above with three pine species, and most inter-species comparisons of development on sands, indicate that Type 1 responses are more common than Type 2. Thus, some confidence can be placed in the attribution of Type 2 responses, entailing losses of plantation productivity between rotations on sandy soils, to a change in site rather than to any change in genotype.

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