SEEDLING GROWTH IN TANEKAHA (*PHYLLOCLADUS TRICHOMANOIDES*): EFFECTS OF SHADE AND OTHER SEEDLING SPECIES

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ABSTRACT

Seedlings of tanekaha (**Phyllocladus trichomanoides**) were grown alone and in a mixture with kauri (**Agathis australis**), mapau (**Myrsine australis**) and lancewood (**Pseudopanax crassifolius**) seedlings under four levels of shading in a glasshouse. Growth response of tanekaha was similar in both experiments. Seedling dry weight increment was linearly related to light intensity for all four species in the range 1.7% to 33% full daylight. Growth rates of the shrub hardwood species (mapau and lancewood) were superior to those of the softwoods (tanekaha and kauri) over the whole range of illumination. It is suggested that the very slow growth rates of the softwoods under shaded conditions, compared to many hardwoods, partly explain the general failure of softwood regeneration in mature primary forest and their patterns of establishment in secondary scrub and forest communities.

INTRODUCTION

Young seedlings of tanekaha (*Phyllocladus trichomanoides* D.Don), an unusual and valuable New Zealand softwood, are sufficiently numerous and widespread in several types of indigenous scrub and forest, to suggest that seed production, dispersal and germination do not involve serious limitations for its regeneration. Factors affecting seedling establishment and growth, however, appear to be more crucial in determining its survival.

It is commonly observed of the regeneration of native softwoods in both forest and scrub communities that their numbers diminish in relation to increased density of shrub hardwoods and tree ferns and vice versa (Cameron, 1959). In the fire induced *Leptospermum* scrub and secondary forests of Northland, tanekaha, often with kauri (*Agathis australis*) occurs as "all-age" populations on elevated sites (crests and sides of ridges and spurs) but is infrequent or absent from lower slopes and valley situations where shrub hardwoods and tree ferns are established in profusion (McKelvey and Nicholls, 1959; Pook, 1978). Seedlings of tanekaha and several other softwoods have been observed to be suppressed under dense regrowth of shrub hardwods and ferns in scrub and forest communities of the Central North Island (Beveridge, 1973). Tanekaha, like several other principal softwoods, also fails to maintain itself where it occurs in older virgin forests, i.e., the large crops of seedlings that periodically appear in the vicinity of parent trees do not persist.

These several aspects of the behaviour of tanekaha and other forest tree species appear to reflect the influence of shade on seedling and subsequent early stages of development.

Cockayne (1928) postulated that "the most important principle underlying succession in New Zealand forests is the relation of the different species to light." This hypothesis has seldom been critically examined since it was first enunciated.

Bieleski (1959a) found young seedlings of kauri and tanekaha to occur "optimally" at quite low light intensities (*c.* 4% of full daylight) in a "semi-mature" *Leptospermum* scrub community. In glasshouse experiments (Bieleski, 1959b), however, it was shown that growth of young kauri seedlings responded to increased illumination up to 40% of full daylight without approaching a limiting value, indicating that factors other than light (e.g., insolation and soil dessication) were limiting seedling establishment at higher light intensities in the scrub community. No similar evaluation of the growth response of seedlings has been published for any other indigenous forest tree species.

The present study is primarily concerned with determining the effects of shade on growth of young tanekaha seedlings. In order that the results might be discussed and applied in a wider ecological context, however, comparisons were also made between tanekaha, kauri and two shrub hardwoods — mapau (*Myrsine australis*) and lancewood (*Pseudopanx crassifolius*) under similar conditions.

METHODS AND MATERIALS

Seedlings were grown under four levels of shading in the glasshouse. A thin coat of lime applied to the underside of the glasshouse roof provided diffuse even illumination equivalent to one-third of full daylight at bench height. This was used as the first level of shading. Three lath screens with nominal transmission factors of 0.5, 0.25 and 0.05 were placed above seedlings on the centre bench to obtain other levels of shading. Thus, the combination of glasshouse roof and lath screens provided four shade treatments under which corresponding levels of illumination were 0.33, 0.17, 0.08 and 0.017 r.l.i. (light intensity relative to full daylight).

Populations of young tanekaha, mapau and lancewood seedlings that had foliage developed little beyond the cotyledonary leaf stage were gathered from beneath parent trees in forest and scrub at Swanson in the Waitakere Ranges. Kauri seedlings at a similar early stage of growth raised under shade in an open nursery were obtained from the Forest Research Institute, Rotorua. The roots of tanekaha and kauri seedlings were well nodulated. The seedlings of each species population were sorted to even size before being planted out into boxes filled with a free draining potting mixture consisting of four parts clay loam, two parts sand and one part of well-decomposed humus. The seedlings were held under shade house conditions for three weeks to allow establishment before being allocated to treatments.

Two experiments were carried out. In the first tanekaha seedlings alone were grown under each of the four treatments for 200 days from 1 December to 19 June inclusive. Two replicate boxes each containing 40 seedlings were allotted to each treatment. Soil was maintained in continuously moist condition by watering twice daily. Weeds were removed as they appeared and a full nutrient solution was applied at intervals to prevent mineral deficiencies from arising. Precautions were taken to eliminate position effects in the treatments. Replicate boxes were rotated and their positions were interchanged frequently within treatments. Treatments were moved systematically through four centre bench locations at weekly intervals. The lath screens were painted white outside, blackened inside and ventilated as much as possible to minimise temperature differences between treatments.

In the second experiment tanekaha, kauri, mapau and lancewood seedlings were grown in a mixture under similar treatments from 1 August to 2 April inclusive. Twenty-one seedlings of each species were planted in a predetermined pattern so that individuals of any one species occupied similar positions to the others in a box. Again, two replicate boxes were allocated to each treatment. Position effects and environmental differences within and between treatments were nullified by procedures prescribed for the first experiment. Because of their relatively rapid growth in high light mapau seedlings threatened to over-top the other species and so were harvested (shoots only) from all treatments after 150 days' growth (i.e., on 28 December). Seedlings of the other three species were harvested after 243 days' growth.

At harvest, seedling root systems were freed from soil while sluicing gently with water and they were finally cleaned in water using a soft brush. Stem lengths were measured before seedlings were oven dried to constant weight at 95°C. After equilibration in a dessicator for 24 hours or more dry weights of component parts were determined.

RESULTS

For practical convenience the results of the two experiments are presented together. Seedling mortalities were mainly due to attacks by tortricid caterpillars rather than treatment effects. Morphological differences in seedlings grown under the different levels of shading were most obvious on tanekaha and lancewood but were to a large extent ontogenetic in character, juvenile foliage being produced on faster growing seedlings in high light treatments ahead of others grown in low light.

Data from the two experiments are summarised in Table 1. The response of tanekaha seedlings to reduction in shading was similar, whether grown alone or together with the other species. Mean stem length, total and component dry weights increased significantly between successive treatments. The proportions of root and shoot developed on tanekaha seedlings were not, however, consistent. Root/shoot ratios were higher and increased with reduction in shade in the first experiment but were similar in all treatments of the second.

Data for seedlings of the other three species show that their response to shading was in most respects similar to that of tanekaha. Mean total dry weight increment was linearly related to degree of shading in each case (Fig. 1). Shoot growth rates calculated according to Blackman's (1919) formula are plotted in relation to levels of illumination in Fig. 2. It should be noted that the shrub hardwood seedlings were initially of much smaller size and average dry weight than either tanekaha or kauri but showed more vigorous growth over the whole range of light intensities. Growth rates of mapau seedlings over the relatively short period of 150 days are in impressive contrast to the growth rates of the other three species for the experimental period. Relative growth rates are similar whether calculated on the basis of total seedling dry weights

TABLE 1—Effect of shade on growth of tanekaha, kauri, lancewood and mapau seedlings. r.l.i. — light intensity relative to full daylight; Figures in parentheses — values of D, significant difference between means ($P < .05$) — Snedecor's modification of Turkey's D (Snedecor, 1956, p. 251).

	Treatment (r.l.i.)	n	Stem Length (mm)	Total	Dry Weight (g) Shoot	Leaf	Stem	Root	Root/ Shoot
Tanekaha Exp. 1	.017	66	54.2	0.0412	0.0301	—	—	0.0111	0.369
	.08	64	65.4	0.1275	0.0969	—	—	0.0306	0.315
	.17	66	80.3	0.3478	0.2367	—	—	0.1111	0.468
	.33	65	104.7	0.7421	0.4908	—	—	0.2513	0.512
			(3.397)	(0.0450)	(0.0319)			(0.0177)	
Exp. 2	.017	31	81.8	0.1571	0.1211	0.0868	0.0341	0.0360	0.297
	.08	39	112.3	0.4175	0.3247	0.2247	0.0974	0.0928	0.285
	.17	42	138.2	0.7442	0.5765	0.4055	0.1709	0.1675	0.290
	.33	40	171.8	1.2063	0.9583	0.6784	0.2742	0.2560	0.267
			(10.630)	(0.0955)	(0.0801)	(0.0251)	(0.0559)	(0.0179)	
Kauri	.017	35	45.0	0.0689	0.0551	0.0336	0.0215	0.0139	0.202
	.08	39	60.0	0.1402	0.1141	0.0793	0.0350	0.0272	0.238
	.17	36	73.9	0.2375	0.2003	0.1401	0.0602	0.0372	0.186
	.33	38	90.9	0.4743	0.3895	0.2653	0.1129	0.0844	0.217
			(3.711)	(0.0249)	(0.0213)	(0.0169)	(0.0060)	(0.0051)	
Mapau	.017	35	44.1	—	0.0302	0.0171	0.0127	—	—
	.08	38	76.3	—	0.0916	0.0642	0.0271	—	—
	.17	36	113.2	—	0.2040	0.1449	0.0591	—	—
	.33	36	121.1	—	0.3432	0.2474	0.0953	—	—
			(7.216)		(0.0271)	(0.0193)	(0.0079)		
Lancewood	.017	24	45.4	0.0298	0.0235	0.0142	0.0094	0.0062	0.264
	.08	34	52.6	0.0726	0.0572	0.0407	0.0162	0.0156	0.273
	.17	36	58.6	0.1943	0.1611	0.1253	0.0412	0.0359	0.223
	.33	32	73.8	0.3716	0.3090	0.2312	0.0746	0.0646	0.210
			(3.610)	(0.0284)	(0.0219)	(0.0180)	(0.0044)	(0.0044)	

or dry weights of seedling components and hence, the comparison of mapau shoot growth rates with total seedling growth rates of the other species is quite valid.

DISCUSSION

Comparative experiments are of proven value in several areas of plant ecological research (Grime, 1965) but they are particularly desirable in studies such as the present one, which are carried out in "semi-controlled" environments. Without comparisons made with other ecologically associated species under such conditions the responses of tanekaha seedlings to various shade treatments would have quite limited implications.

Growth responses of tanekaha grown in isolation (Experiment 1) and previous data on the effects of light intensity on kauri seedlings (Bieleski, 1959b) are useful criteria for the comparative study (Exeperiment 2). The generally consistent response of tanekaha in two experiments and the behaviour of kauri (similar to previous data) provide a reasonable basis for the assumption that sharing the soil medium with the shrub

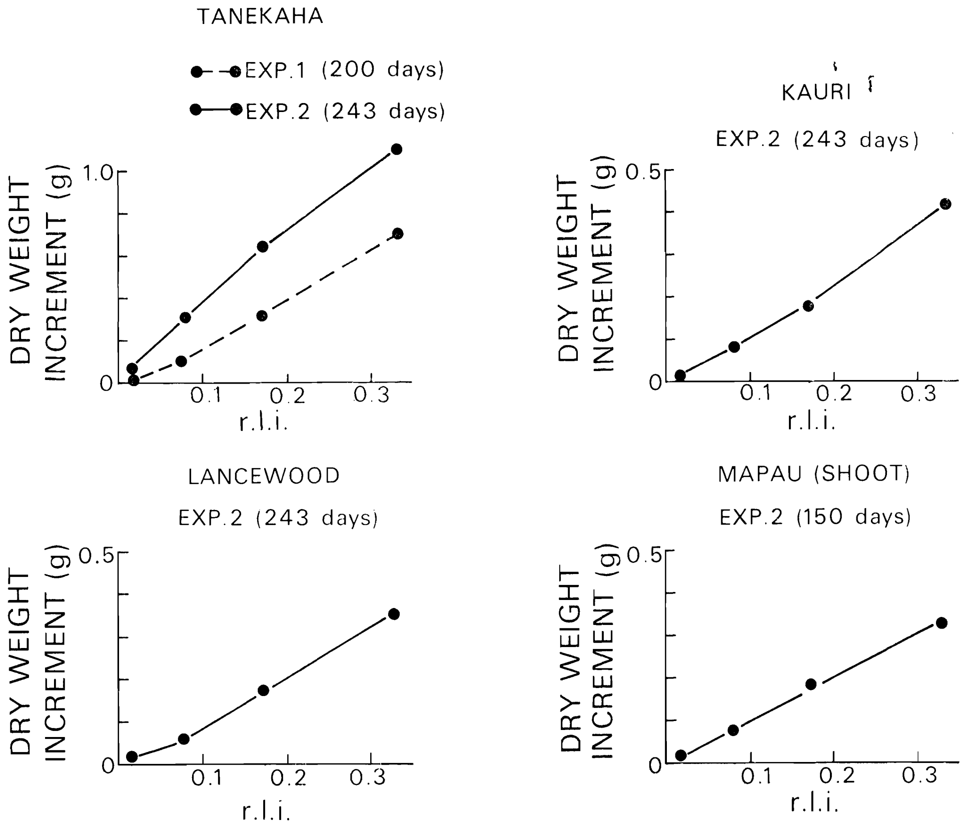

FIG. 1—Effect of shade on dry weight increment of tanekaha, kauri and lancewood seedlings and mapau shoots.

hardwood species had not limited the growth of the softwood seedlings (though this would not be expected to continue indefinitely). However, the differences in tanekaha root/shoot ratios between the two experiments should be noted. In the comparative study, root/shoot ratios for tanekaha, kauri and lancewood are similar (mostly between 0.2 and 0.3) and concur with ratios obtained from Bieleski's (1959b) kauri data. Thus, it seems that conditions peculiar to the first experiment (perhaps seasonal) had stimulated more root growth than usual in tanekaha seedlings but had not altered the overall response to shading. Since seedling growth increment was linearly related to shading for each species it is unlikely that root competition or antagonisms were significant in any of the treatments of the comparative experiment.

From this latter result and in other aspects of seedling growth it is apparent that the response of kauri seedlings to light (Bieleski, 1959b) is not unique. Tanekaha, mapau and lancewood seedlings, like kauri, are capable of surviving and growing (though with differing vigour) at quite low light intensities (<0.02 r.l.i.) and their response to increased illumination up to 0.33 r.l.i. shows no sign of approaching an upper limit for growth. The bias in distribution of young tanekaha seedlings to deep shade in semi-mature *Leptospermum* scrub must be explained, as for kauri (Bieleski,

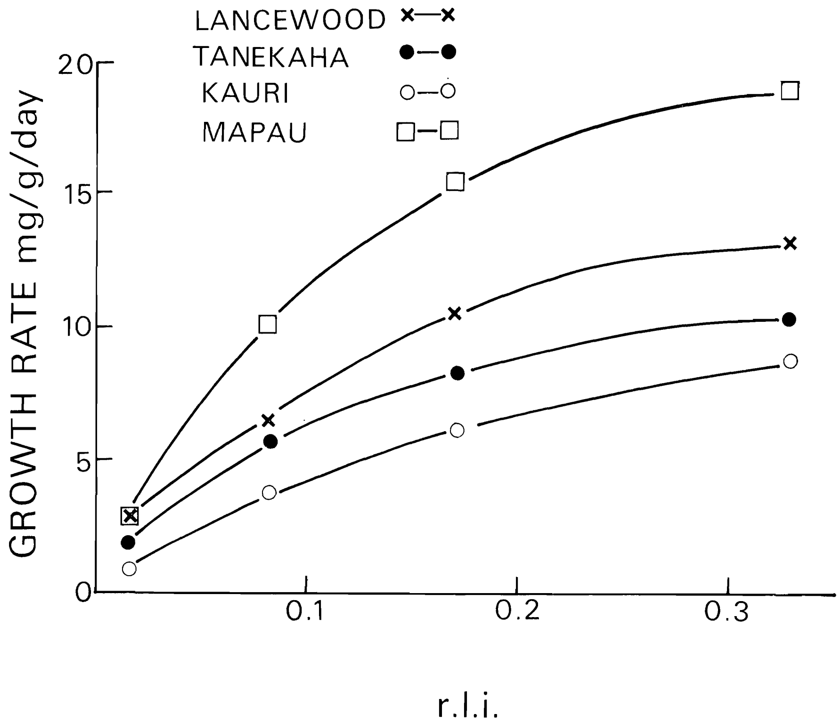

FIG. 2—Effect of shade on relative growth rate of seedlings (tanekaha, kauri and lancewood — 243 days' growth; mapau 150 days' growth).

1959a) by the influence of environmental factors other than light limiting seedling establishment at higher light intensities. In practice seedlings of tanekaha, kauri and several other native forest softwoods are grown successfully under 50% or more daylight in favourable nursery conditions. Tanekaha seedlings planted out into a variety of scrub and forest environments in Central North Island have also been reported to grow fastest in "well-lit" sites (N.Z.F.S. 1977). Growth rates of mapau and lancewood seedlings would likewise be expected to improve with illumination increased beyond 0.33 r.l.i.

Although mapau and lancewood are not "principal" forest hardwoods their response to shading is nevertheless of some ecological significance and application. Both shrub hardwoods are widely distributed throughout New Zealand, occurring in a variety of lowland scrub and forest communities where they maintain "all-age" populations in varying degrees of shade. They are in several respects typical of a large group of arborescent shrub hardwoods that Cockayne (1928; p. 152) lists together with kauri, tanekaha and most of the principal forest trees as "light-demanding or, some of them shade-tolerating species which become established in bright light". A capacity to establish and grow at the low energy levels which prevail under deep shade at the forest floor is more or less obligatory for the majority of plants, including seedlings of dominant trees, if they are to maintain their status and survive in lowland forest communities.

The very slow growth rate of native softwood seedlings compared with those of many other arborescent species may not be adequate in what must be a strongly competitive situation, particularly at low light intensities. "Shade persistence" often noted of softwood seedlings under virgin forest appears to be of little significance for maintenance of softwood populations as there are few stems intermediate in size between seedlings and mature trees in those forests. "Shade *persistence*" is not necessarily equated with "shade *tolerance*" (cf. Ogden, 1971). Persistence of seedlings for long periods without any appreciable growth occurring merely reflects the low energy status and stability of conditions in shade at the forest floor. Poorly developed root systems of softwood seedlings in such environments (Cameron, 1963) underlines their susceptibility to physical and biological stresses which, though they occur infrequently, are inevitable and eliminate young and old "stagnating" individuals alike. If light conditions improve with the appearance of canopy gaps vigorous shrub hardwoods and other species respond more readily than the softwoods and may eventually suppress the latter (Beveridge, 1973).

The low compensation points for seedling growth (*c. 0.01* r.l.i.) that can be inferred from growth data for the four species studied (Fig. 1) constitute only one aspect of their adaptation to shade. "Shade tolerance" obviously varies widely if measured in other terms such as relative growth rate and productivity. Shrub hardwoods, such as mapau, which can achieve relatively rapid growth over a wide range of shade conditions, including deep shade, can be more readily accepted as "shade tolerant".

Intrinsically slow growth rates characteristic of indigenous softwoods may not always be a disadvantage. As pointed out by Parsons (1968) "environmental selection of plants with slow growth rates is a frequent and simple form of adaptation to limiting levels of environmental factors". This would appear to be well substantiated by the patterns of regeneration of tanekaha and kauri in many *Leptospermum* scrub communities in Northland where conditions for growth and establishment of forest species, at least during early stages of succession (cf. Mirams, 1957) are difficult and improve only gradually. With a low physiological requirement for nitrogen and phosphorus (Peterson, 1962) tanekaha and kauri establish early under scrub on relatively low quality sites, mainly dry exposed ridges and ridge sides, while more mesophyllous shrub hardwoods and tree ferns occupy sheltered slopes and valleys with relatively moist fertile soils. What are in some respects the less favourable sites are the foci of the best examples of regeneration of the two softwoods.

There is little difficulty in accepting that other factors beside shade influence the patterns of regeneration of forest tree species. However, until a good deal more information is available on the growth responses and behaviour of many more forest components in respect of this attenuation of the primary energy source, knowledge of the effects of other factors could be greatly limited in its application. The assessment of responses of many forest components, both dominant and subordinate, to shade would appear to be fundamental to understanding of the dynamics of most indigenous forest communities and for resolving some of the problems of failure in natural maintenance of some species. Comparative experiments similar to, but perhaps more elegant than the present one, involving study of groups of associated and competing forest species are a useful starting point in supplying necessary quantitative information.

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REFERENCES

BEVERIDGE, A. E. 1973: Regeneration of podocarps in a Central North Island Forest. **N.Z. J. For. 18(1):** 23-35.

BIELESKI, R. L. 1959a: Factors affecting growth and distribution of kauri (**Agathis australis** Salisb.). I. Effect of light on the establishment of kauri and of **Phyllocladus trichomanoides**. **Aust. J. Bot. 7:** 252-67.

——— 1959b: Factors affecting growth and distribution of kauri (**Agathis australis** Salisb.). II. Effect of light intensity on seedling growth. **Aust. J. Bot. 7:** 268-78.

BLACKMAN, V. H. 1919: The compound interest law and plant growth. **Ann. Bot. Lond. 33:** 353-60.

CAMERON, R. J. 1959: The management potential of the native forests of North Auckland. **N.Z. J. For. 8(1): 46-55.**

——— 1963: A study of the rooting habits of rimu and tawa in pumice soils. **N.Z. J. For. 8(5):** 771-85.

COCKAYNE, L. 1928: "The Vegetation of New Zealand" 2nd ed. Engelmann, Leipzig. 456 pp.

GRIME, J. P. 1965: Comparative experiments as a key to the ecology of flowering plants. **Ecology 46(4):** 513-5.

McKELVEY, P. J. and NICHOLLS, J. L. 1959: The indigenous forest types of North Auckland. **N.Z. J. For. 8(1):** 29-45.

MIRAMS, R. V. 1957: Aspects of the natural regeneration of the kauri (**Agathis australis** Salisb.). **Trans. Roy. Soc. N.Z. 84:** 661-80.

N.Z.F.S. 1977: Report of Forest Research Institute, 1976 p. 77. N.Z. Forest Service, Wellington.

OGDEN, J. 1971: Studies on the vegetation of Mount Colenso (New Zealand). 2. The population dynamics of red beech. **Proc. N.Z. Ecol. Soc. 18:** 66-75.

PARSONS, R. F. 1968: The significance of growth-rate comparisons for plant ecology. **American Naturalist 102(928):** 595-7.

PETERSON, P. J. 1962: Mineral nutrition of **Agathis australis** Salisb., the kauri: Part 1 — Effects of deficiencies of essential elements on the growth and foliar mineral composition of seedlings. **N.Z. J. Sci. 5:** 141-64.

POOK, E. W. 1978: Population and growth characteristics of tanekaha in **Leptospermum** scrub and secondary forest of the Waitakere Ranges, Auckland, New Zealand. **N.Z. J. Bot. 16:** 227-34.

SNEDECOR, G. W. 1956: "Statistical Methods". 5th ed. The Iowa State College Press, Ames, Iowa.