

ACCUMULATION AND PARTITIONING OF DRY MATTER IN PINUS RADIATA AS RELATED TO STAND AGE AND THINNING

P. N. BEETS and D. S. POLLOCK

Ministry of Forestry, Forest Research Institute, Private Bag, Rotorua, New Zealand

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ABSTRACT

Pinus radiata D. Don dry matter and leaf area were measured at the Puruki site annually between ages 2 and 12 years in stands undergoing contrasting thinning. Current dry matter production and its partitioning to leaves, branches, and stems were estimated.

In an unthinned stand stocked at 2200 stems/ha, 230 t dry matter/ha accumulated by age 12 compared with 75 t/ha in a stand thinned to 160 stems/ha; however, the mean dbh in the unthinned stand was only 22 cm compared with 37 cm in the heavily thinned one. Basal area increment peaked at over 10 m²/ha/year at age 4 but decreased to 3–4 m²/ha/year by age 12, irrespective of thinning. Without thinning, basal area attained almost 60 m²/ha by age 12, while the removal of 90% of the trees in two thinning steps reduced basal area by 70%. Leaf area (all surfaces) index peaked at 34 at age 6 but declined to 20 with increase in stand age. Above-ground production varied between 2 and 40 t/ha/year depending on stand age and thinning treatment. Thinning prevented most branch and tree mortality evident in the unthinned stand.

Between ages 2 and 12 years, partitioning of annual above-ground dry matter production to leaves decreased from 40% to less than 20%, to stem increased from 35% to 60%, and to branches remained constant at around 23%. Thinning had little measurable effect on partitioning. Production above-ground increased, at a given leaf area index, with stand age. A shift in partitioning from roots to stem wood, rather than an increase in the efficiency of production *per se*, probably underlies this result. Tentative estimates of partitioning based on total current dry matter production were developed for **P. radiata** growing without moisture or nutrient limitations.

Keywords: dry matter production; leaf area; growth partitioning; thinning; physiological aging; biomass; root : shoot ratio; primary productivity; **Pinus radiata**.

INTRODUCTION

Pinus radiata is the most widely planted production forestry tree species in New Zealand; however, little is known of the factors influencing partitioning of its growth to different tree components. Our lack of understanding of fundamental growth processes and controls limits our ability to predict accurately growth of any tree species (Cannell 1985; Madgwick 1985). Mechanistic models of forest growth include partitioning of dry matter production to leaves, branches, stems, and roots (Rook *et al.*

1985). Radiation interception, photosynthesis, respiration, water use, and nutrient uptake are influenced either directly or indirectly by partitioning. Partitioning also reflects sink strengths, and so a basic understanding of partitioning is essential for the development of mechanistic models of forest growth (Causton 1985).

Dry matter partitioning to all the components of trees has been described for only a few forests, and never over time (Cannell 1985). Noteworthy are the large differences in partitioning found, but whether these reported differences are due to endogenous factors, such as species and age, or exogenous factors, such as the physical environment and management, or simply errors of estimation is still uncertain (Cannell 1985).

Tree age effects need to be taken into account when interpreting the role of other factors on partitioning, but various lines of evidence on partitioning above-ground yield conflicting results. For instance, partitioning to stems was constant or declined with age after canopy closure in some conifer stands (Satoo & Madgwick 1982; Cannell 1985) but increased in *P. radiata* (Madgwick & Oliver 1985). This shift to stems in *P. radiata* was quite marked, with an associated decrease in partitioning to leaves from 20% to 10% between stand ages 9 and 13 years. Indirect evidence of the effects of age on partitioning comes from an examination of over 100 biomass studies undertaken for *P. radiata* (Madgwick 1985); leaf production decreased from 10 to 5 t/ha/year within the first 10 years, during which time stem production would not be expected to decline. Furthermore, *P. radiata* cuttings of the same chronological age were morphogenetically dissimilar depending on the age of the parent material (Menzies & Klomp 1987).

Objectives

This paper is based on a major research effort to examine dry matter production and partitioning in stands of *P. radiata*, without moisture or nutrient limitations to growth. Estimates of the dry matter content and derived current annual dry matter production and partitioning estimates to leaves, branches and stems are reported. These estimates were repeated annually for 10 years, commencing 2 years after planting, for stands subjected to contrasting thinning treatments. Results are discussed in the light of root production estimates made at the end of the study period.

METHODS

Site Description

Puruki catchment (more fully described by Beets & Brownlie 1987) is part of the Purukohukohu Experimental Basin located in the Paeroa Range in the central North Island of New Zealand (Fig. 1). Slopes are flat to steep (between 0° and 40°), elevation varies from 510 to 750 m, with the average aspect to the east (Fig. 1). Soils are classified as yellow-brown pumice soils derived from rhyolitic ash (Taupo Pumice) laid down about A.D. 200 (Vucetich & Pullar 1969; NZ Soil Bureau 1968).

Meteorological data were collected on site between 1976 and 1985. Precipitation was evenly distributed and averaged 1500 mm/year, ranging between 1150 and 2010 mm. Annual average temperature ranged between 9° and 11°C with a January–February average maximum of 15°C and a July–August average minimum of 5°C. Solar irradiance varied from 4.8 to 5.3 GJ/m²/year and averaged 5.0 GJ/m²/year.

Puruki is divided into three subcatchments (Fig. 1): Toru (c. 13.8 ha) drains the western higher elevations, Rua (c. 8.7 ha) the central part, and Tahī (c. 5.9 ha) the lower elevations to the east. An additional area (c. 6.0 ha) in the south-eastern corner of Puruki was managed as for Tahī.

Originally supporting podocarp/hardwood forest, which still covers most of the Paeroa Range today, Puruki was converted from seral scrub to ryegrass/clover pasture in 1957 after less successful attempts at pasture development in the 1920s. Regular applications of cobaltised superphosphate to stimulate clover and nitrogen fixation (Selby 1971) contributed to the high fertility of Puruki (Beets & Brownlie 1987).

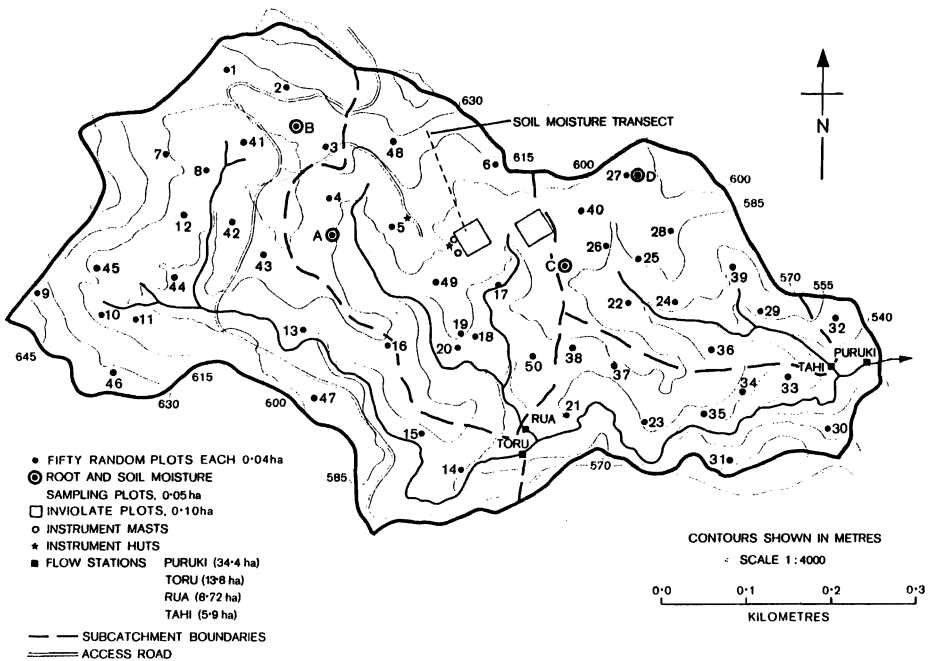


FIG. 1—Puruki experimental catchment, originally in ryegrass/clover pasture then planted with *Pinus radiata* seedlings in 1973.

Development of Site

Puruki was uniformly planted with pines in winter 1973 after spraying to kill the dense pasture grasses. Nursery-raised seedlings of 1-year-old *P. radiata* were planted at 2.4×1.8 m or 2200 stems/ha. Inspection of the site 6 months after planting indicated 80–90% survival in all but the south and west areas of Toru. The low survival there of 10–30% was attributed to planting exposed stock in frosty sunny weather. Blanking and virtual replanting of poorly stocked areas was completed in September 1974.

Stand Management

Each subcatchment at Puruki was managed separately (*see* notes at foot of Table 1). Pruning to 2.2 m height was designed to improve access for stand measurement purposes, without unduly influencing growth. Except for an unthinned area, thinning intensities were initially identical though differing in timing until 1983. Contrasting stockings were then maintained, reflecting a change in management philosophy aimed to provide information under three contrasting conditions, namely,

- (a) The unlimiting condition of continuous open growth in Tahi;
- (b) The limiting condition of canopy closure in Rua;
- (c) An intermediate condition of successive open growth followed by canopy closure in Toru.

It was therefore possible to examine for *P. radiata* at Puruki the potential to occupy space, crown and tree mortality processes, and the recuperative ability of crowns after release from competition.

Stand Measurements

Dry matter content and leaf area (all surfaces) were estimated using a combination of nondestructive and destructive sampling procedures; permanent plots provided basic mensuration data and sample trees provided dry matter relationships for each subcatchment.

Plot number, size, and measurement

Initially, 30 randomly located plots each of 0.01 ha (horizontal area basis) were allocated to the subcatchments in proportion to their area. Plot size was increased to

TABLE 1—Number of *Pinus radiata* trees harvested each year in the Puruki subcatchments (Tahi, Rua, and Toru)

Stand	Number of sample trees by year and age										
	'75 2	'76 3	'77 4	'78 5	'79 6	'80 7	'81 8	'82 9	'83 10	'84 11	'85 12
Tahi	7	3	7	4	4*	10	7	5	7†	7	5
Rua	5	2	5	4	4	4*	7	5	7	7‡	5
Toru	3	11	3	7	7	6	7*	5	7	7§	5
Inviolate¶	0	0	0	0	0	0	0	0	0	0	5
Total harvested	15	16	15	15	15	20	21	15	21	21	20

* Stand pruned to 2.2 m and thinned from 2200 to 550 stems/ha nominal stockings. Assessment plot areas increased from 0.01 to 0.04 ha.
 † Tahi thinned from 550 to 137 stems/ha nominal stockings, and number of assessment plots increased from 10 to 20.
 ‡ Rua assessment plots increased from seven to 10.
 § Toru thinned from 550 to 275 stems/ha nominal stockings, and number of assessment plots increased from 13 to 20.
 ¶ Two unthinned plots within Rua. Plot areas each 0.10 ha throughout, and referred to as inviolate plots.
 Note: Actual stockings are given in Table 5

0.04 ha after the first thinning. From 1983 the number of plots was increased to 50 (Table 1). The number and size of plots were increased to maintain adequate numbers of trees measured for diameter. A part (0.85 ha) of Rua was left unthinned and two 0.10-ha plots were established to monitor development without thinning (inviolable plots).

Tree top height was measured annually using a height pole (to nearest 10 cm) for all trees till 1977 and then for at least five trees per plot till 1979. From 1980 heights were measured with hypsometers using taped distances (Blume-Leiss or Suunto). Height (cm) to the lowest live branch was measured by tape. The diameter at breast height (dbh at 1.4 m) was measured with a diameter tape each year on all assessment plot trees.

For each subcatchment the following variables were calculated by year: mean top height of all measured live trees and mean height to the base of the green crown, calculated as the arithmetic mean tree top height and height to lowest live branch, respectively. Tree basal area, which is the cross-sectional area of the trees measured at breast height (Spurr 1952), was calculated for live trees and live-plus-dead trees. Only live tree basal areas are given but live-plus-dead tree basal areas were required when accounting for stand dry matter losses due to mortality – as described later.

Measurements were made in winter (June-July) each year.

Sample tree numbers, dry matter, and leaf surface area (all surfaces)

The number of sample trees harvested varied with stand age and subcatchment (Table 1). Trees were harvested between May and August each year. Trees were selected at least one plot diameter distant from assessment plots, but otherwise strictly at random.

Each tree was felled at 10 cm height, and measured for total height and dbh. Fascicles directly attached to the stem were collected by leaf age-class (immature, 1-year, 2-year, and > 2 years old) and 10 per leaf age-class were measured for length (Beets 1977). All cones were collected. Dead branches of entirely dead branch clusters at the base of the crown were weighed fresh, the material was cut into approximately 10-cm-long sections, and a sample of known fresh weight was collected. Thirty undamaged fascicles from each leaf age-class were collected from throughout the crown and stored in polythene bags with water to prevent dehydration. Leaf density (dry weight per unit volume) of these fascicles was determined (Beets 1977).

The entire live crown was weighed fresh using procedures that depended on stand age. From 1975 to 1983 (tree heights 1–14 m) the crown was weighed as a whole. From 1983 to 1985 (tree heights 10–22 m) the crown was stratified vertically into 2-m zones, measured from ground level. Branches were trimmed from the stem and weighed by zone. Branches from zones in the lower half of the green crown were divided into two or three matched piles of branches, with one pile weighed fresh and retained for further processing. Branches from zones in the upper half of the crown and from trees prior to 1983 were processed in their entirety as described below.

Branches were processed in the forest by cutting them into approximately 10-cm-long sections and allocating sections to one of the following categories: leaf-bearing twigs by leaf age-class, live bare branch sections, and dead branch sections. Each such

category was weighed fresh. A sample was obtained by dividing each category of material into eighths with the proviso that no sample should weigh less than 1 kg fresh weight.

In the laboratory, fascicles were stripped off the twigs. Fifty branch fascicles per leaf age-class prior to 1983 and 20 per leaf age-class per 2-m height zone were measured for length (Beets 1977). Some of the branches (excluding the dead category) were debarked. Dry weights of all samples were determined after they had dried to constant weight at 65°C in forced-ventilation ovens.

Prior to 1983, the stem was cut into variable length sections each containing three branch cluster nodes. Each section was weighed fresh, and a random sample one-third by length cut. From 1983 to 1985 the stem was cut into 2-m-long sections and weighed fresh, and a disc sample (100 mm thick) was cut from the bottom end of each section. Stem samples were weighed fresh, debarked in the laboratory, and the wood and bark samples oven dried.

Moisture contents were calculated and applied to the fresh weight data, and wood and bark ratios were applied to branch and stem weights. Zonal data were summed to give tree weights. Dead branch weight includes branches in dead branch clusters and dead twigs within the live crown. Leaf weight and area includes stem and branch leaves.

Leaf area of all surfaces was calculated as described by Beets (1977) and Beets & Lane (1987). Leaf area on an all surface basis can be converted to a projected area basis by dividing by the constant, π (Beets & Lane 1987). Reliable individual tree dry matter and surface area data were obtained using these procedures.

Stand Dry Matter Content and Production

Stand dry matter per hectare and leaf area index were computed from the sample tree and plot assessment data using the ratio of means method (Cochran 1963) with basal area as the auxiliary variate. Compared to measured tree weights, the basal area ratio method proved the most consistent of a range of estimators examined (Madgwick 1983). Stand weight estimates were developed using plot assessment data collected from each subcatchment each year and the concomitant sample trees. For the present purposes the loss in precision by maintaining this statistical independence between subcatchments and years was considered to outweigh any benefits from combining data.

Dry matter content and error estimates by different prediction methods were compared using data collected in 1979 and 1985, to give an indication of the accuracy and precision of the stand weight estimates.

Current annual dry matter production was calculated as follows. Leaf production was assumed to equal the weight of 1-year-old fascicles. Leaf production was not adjusted for measured leaf density increases (Beets & Lane 1987) in older leaves because corresponding density decreases occurred immediately prior to leaf abscission (Beets & Pollock 1987). Stem and branch production were calculated as the increase in dry weight between successive years, including mortality losses. The leaf, branch, and stem production estimates were summed to give current annual dry matter production above ground. Using these methods of calculation, stem and branch production estimates in

adjacent years were not independent; however, leaf production estimates were. After increases in plot number or size, production estimates were based on a larger area though not necessarily on more trees.

Production was estimated in the inviolate plot for the 1984–85 increment period as follows. Leaf production was assumed to equal the weight of 1-year-old fascicles in the 1985 sampling. Branch production was calculated from branch mortality and the average annual change in weight of the live branches, using the Rua live branch data collected in 1980 as the age 7 estimate for the inviolate plots. Branch mortality was estimated from annually removed and weighed dead branch clusters formed at the base of the crown of 83 trees from the inviolate plot surrounds in three transects running both along and across the planting lines. Stem production was estimated as the average annual increase in stem weight of the inviolate plots in 1985 using Rua stem data in 1980 as the age 7 estimate for the inviolate plots.

RESULTS

Stand Basal Area and Height

Annual basal area and height development are given in Fig. 2 and 3, and precision of basal area and basal area increment estimates in Table 2. Early differences between subcatchments in basal area and height were followed by parallel development, and reflect establishment rather than site differences between subcatchments. Toru is 1 year behind the other stands because a large part of Toru was replanted in 1974. Without thinning, basal area attained 60 m²/ha. Thinning of Tahi removed 90% of the trees but reduced basal area by about 70% by age 12. Canopy closure and pruning increased the height to base of green crown but thinning prevented further increases.

Basal area increments peaked at around 10 m²/ha/year by age 4 but then decreased to around 3–4 m²/ha/year by age 12, regardless of thinning intensities.

The mean, minimum, and maximum diameters (dbh) increased with thinning intensity (Table 3). Light pruning and different intensities of thinning did not influence mean height growth (Fig. 3). However, mean height growth decreased with age in unthinned stands. The height data suggest a site index, or more appropriately a height index, of around 35 m at age 20 (Burkhart & Tennent 1977).

Between-plot variations of basal area and basal area increment were large initially but decreased quickly with age as trees increased in height above 1.4 m (Table 2).

Sample Tree Characteristics

Mean size and weight of sample trees in 1979, before any thinning had occurred, and in 1985 are given in Table 4. In 1985 the mean dbh and component weights increased with thinning intensity, with leaf and branch weights on average at least four times and stems two times heavier in Tahi than in the inviolate stand. The mean diameter of the 1985 sample trees (Table 4) was within 5% of those on the corresponding assessment plots (Table 3).

STOCKING

TAHI	1970	1960	1960	1950	1950 495	495	495	495	495 159	156	156
RUA	1843	1843	1843	1843	1843	1843 550	550	550	550	550 577	575
TORU	2123	2092	1969	1969	1962	1962	1962 561	549	540	538 292	292
INVIOULATE	1975	1935	1930	1930	1910	1905	1875	1750	1645	1610	1550

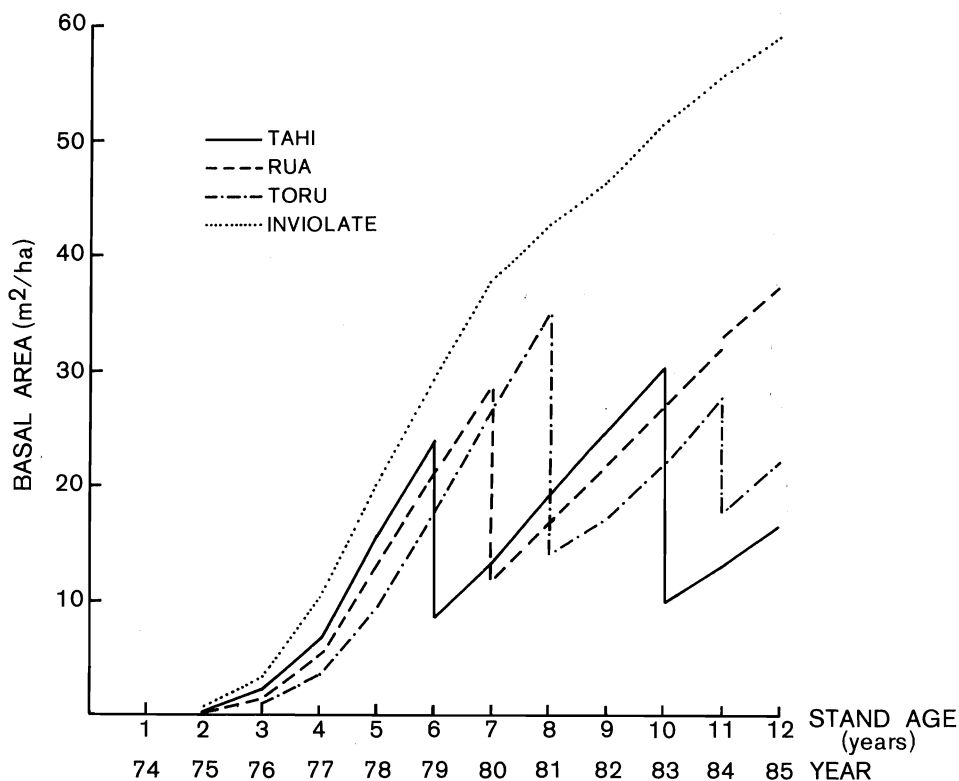


FIG. 2—Stocking (stems/ha) and basal area (m²/ha) of live trees by subcatchment at Puruki.

Stand Dry Matter Content Over Time

The component dry matter content of the Puruki stands as at June each year is presented in Table 5. Total leaf weight peaked at 12–19 t/ha by age 6 but tended to decline thereafter, both with and without thinning. Thinning and pruning at age 6 to 8 years reduced leaf weight to about 4 t/ha but canopies recovered within 4 years to unthinned levels, except in Toru where further thinning prevented this. Live branch

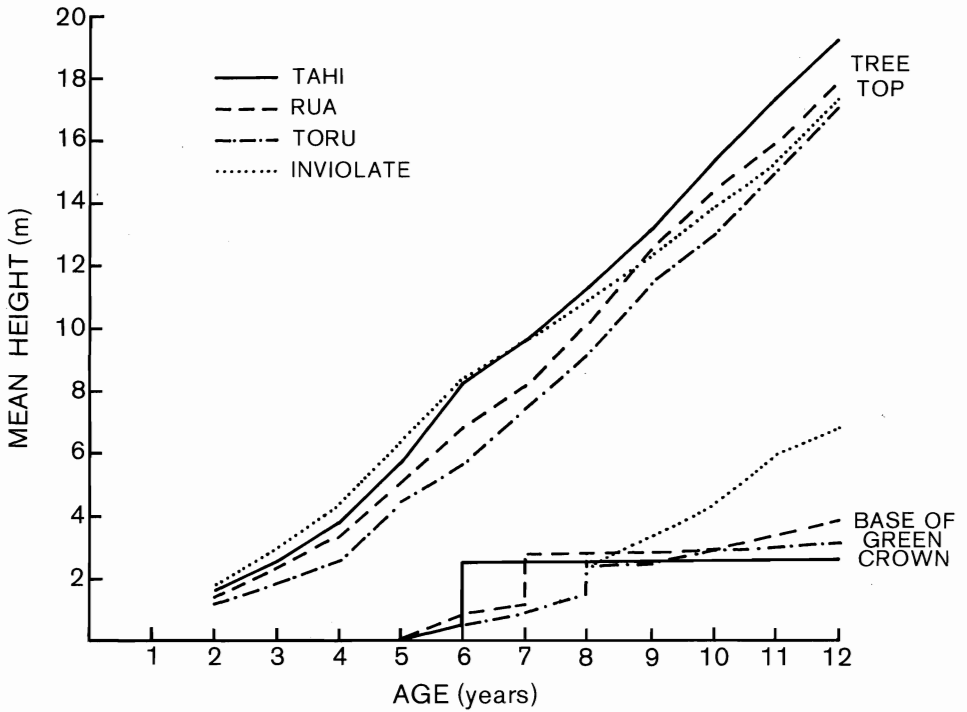


FIG. 3—Mean height of live trees and height to base of green canopy by sub-catchment at Puruki.

TABLE 2—Assessment plot mean basal area (m²/ha) and basal area increment (m²/ha/year) at the start, middle, and end of the measurement period

Stand		Age (years)					
		3 BA	2-3 BAI	6 BA	5-6* BAI	12 BA	11-12 BAI
Tahi	Mean	2.2	1.9	24.2	8.4	16.4	3.5
	SE%	20	19	6	3	5	5
Rua	Mean	1.1	0.9	21.1	8.1	37.3	4.3
	SE%	23	24	7	4	4	6
Toru	Mean	1.0	0.9	17.5	8.3	22.0	4.2
	SE%	30	29	12	8	3	4
Puruki	Mean	1.4	1.23	20.6	8.3	—	—
	SE%	16	615	6	3	—	—

* Before any thinning had occurred. At age 12 stands were at contrasting stockings.

TABLE 3—Live tree diameter at breast height by subcatchment at Puruki at age 12 (1985), based on trees in assessment plots

Stand	dbh (cm)		
	Mean*	Minimum	Maximum
Tahi	36.6	18.8	48.0
Rua	28.7	13.1	40.5
Toru	31.0	19.1	44.8
Inviolata	22.0	8.8	39.9

* Mean diameter is defined as the diameter of the tree with mean basal area (Spurr 1952).

TABLE 4—Sample tree arithmetic mean diameters at breast height, and arithmetic mean leaf, branch, and stem weight by subcatchment at Puruki in 1979 (age 6 years*) and 1985 (age 12). Sample trees were selected at random, though at least one plot diameter distant from assessment plots

Stand	dbh (cm)		Leaf weight (kg)		Branch weight (kg)		Stem weight (kg)	
	6	12	6	12	6	12	6	12
	Tahi	10.4	35.5	7.0	42.2	7.9	113.0	10.4
Rua	13.5	28.0	10.9	23.8	14.4	75.2	16.9	179.9
Toru	10.2	29.7	6.2	27.4	7.5	49.0	10.5	170.5
Inviolata	—	23.2	—	10.3	—	24.1	—	124.5
Mean	11.1	29.1	7.7	25.6	9.5	65.3	12.2	186.6
SE	0.9	1.5	1.7	3.4	2.5	11.4	2.2	17.9

* Stands all unthinned at age 6, but at contrasting stockings at age 12.

weight behaved much the same as described for leaves; however, the peak was delayed and, unlike for leaves, seemed to depend on stocking. For example, the unthinned stand attained 30 t/ha but Rua, at 550 stems/ha, attained 44 t/ha by age 12. The Rua value seems to be an over-estimate. Because Tahi and Toru were not closed at age 12 the peak live branch weight at these lower stockings had still to be attained. Stem weight exceeded 160 t/ha in the unthinned stand at age 12. In contrast, Tahi stem weight was only 45 t/ha at age 12. The percentage of stem weight composed of bark decreased with age from around 28% to 10% regardless of thinning intensity.

Above-ground dry matter attained 230 t/ha in the unthinned stand, but only 75 t/ha in Tahi (Fig. 4). The fraction of stem increased with time; however, thinning delayed this development with the stand dry matter content composed more of crown materials in thinned stands (Fig. 4). Pruning removed a greater proportion of live crown from Tahi than from Rua, while pruning in Toru removed mostly dead branches. The effects of pruning on growth were considered to be minimal, as discussed by Beets & Brownlie (1987).

TABLE 5—Dry matter content (t/ha) of *Pinus radiata* stands at Puruki measured annually from ages 2 to 12 years old

Stand	Stocking (stems/ha)	Age (years)	Stem wood	Stem bark	Dead branch	Branch wood	Branch bark	Leaves >2yr	Leaves 2 yr	Leaves 1 year	Leaves immature	Leaves total	Cones
Tahi	1970	2	0.5	0.2	0.0	0.3	0.2	0.0	0.2	0.5	0.2	0.9	0.0
	1960	3	2.5	0.4	0.0	1.1	0.6	0.0	0.2	2.0	0.1	2.4	0.0
	1960	4	7.3	1.3	0.1	4.9	2.0	0.0	1.0	6.7	0.3	8.0	0.0
	1950	5	15.1	2.0	0.0	10.7	3.4	0.0	3.1	9.4	0.0	12.5	0.1
	1950	6	24.4	3.8	0.2	15.9	5.4	2.8	6.1	10.1	0.0	18.9	0.0
	495	6	8.6	1.3	0.0	3.5	1.1	0.2	0.6	2.8	0.0	3.6	0.0
	495	7	16.3	2.0	0.1	6.3	1.6	0.0	1.1	3.6	0.1	4.8	0.1
	495	8	28.8	3.4	0.1	11.8	2.9	0.2	2.3	6.0	0.0	8.6	0.0
	495	9	45.6	5.0	0.5	16.9	4.1	0.4	4.1	7.1	0.2	11.7	0.5
	495	10	54.8	6.1	1.5	25.2	6.0	0.3	4.6	6.6	0.0	11.4	0.6
	159	10	18.2	2.0	0.5	8.4	2.0	0.1	1.5	2.2	0.0	3.8	0.2
	156	11	30.3	3.0	0.4	11.5	3.3	0.6	1.4	2.5	0.0	4.4	0.5
Rua	156	12	40.3	4.5	0.8	18.6	0.0*	0.5	1.7	4.8	0.0	7.0	0.8
	1843	2	0.3	0.1	0.1	0.1	0.0	0.0	0.1	0.2	0.2	0.5	0.0
	1843	3	2.0	0.4	0.0	1.0	0.6	0.0	0.0	2.0	0.1	2.1	0.0
	1843	4	4.7	0.8	0.0	2.3	1.0	0.5	3.6	3.6	0.0	4.2	0.0
	1843	5	12.1	1.7	0.4	6.4	2.4	0.2	3.2	6.7	0.0	10.0	0.0
	1843	6	20.9	2.7	0.4	15.8	4.3	1.8	5.6	7.8	0.0	15.2	0.0
	1843	7	37.9	4.3	2.3	13.1	3.4	0.0	3.3	6.6	0.1	10.0	0.7
	550	7	15.9	1.8	0.2	4.4	1.1	0.0	1.0	2.1	0.0	3.2	0.0
	550	8	26.9	2.7	0.4	7.0	2.2	0.0	0.9	4.6	0.1	5.6	0.1
	550	9	35.7	3.8	1.2	9.6	2.5	0.0	0.9	6.3	0.0	7.3	0.1
	550	10	55.1	6.0	1.6	16.8	4.8	0.0	3.1	6.1	0.0	9.2	0.5
	550	11	69.0	7.5	3.3	22.5	5.7	1.9	3.9	4.4	0.0	10.2	1.2
Toru	577	11	71.2	7.7	3.4	23.2	5.9	2.0	4.0	4.6	0.0	10.5	1.3
	575	12	95.8	9.2	3.0	43.9	0.0*	3.0	3.8	6.4	0.0	13.2	2.4
	2123	2	0.2	0.1	0.0	0.1	0.0	0.0	0.0	0.2	0.1	0.3	0.0
	2092	3	1.1	0.2	0.0	0.4	0.3	0.0	0.0	0.9	0.1	1.0	0.0
	1969	4	3.2	0.5	0.0	1.6	0.7	0.0	0.2	2.9	0.0	3.0	0.0
	1969	5	10.2	1.4	0.1	5.8	2.1	0.1	3.0	5.9	0.0	9.0	0.1
	1962	6	17.4	2.5	0.6	11.1	3.3	0.0	3.1	8.5	0.0	11.7	0.0
	1962	7	29.7	3.8	3.5	11.9	3.3	0.0	3.0	7.3	0.2	10.5	0.0
	1962	8	47.8	5.2	2.7	15.1	4.5	0.1	2.3	8.2	0.1	10.8	0.1
	561	8	19.6	2.1	0.5	4.5	1.3	0.1	0.7	2.9	0.0	3.7	0.0
	549	9	26.3	3.6	0.7	7.6	2.4	0.1	1.5	4.2	0.0	5.8	0.0
	540	10	40.5	4.9	0.7	10.3	3.8	0.2	3.2	5.9	0.0	9.3	0.1
538	11	53.7	5.8	2.6	14.7	4.4	1.1	4.7	6.1	0.0	11.9	0.3	
292	11	34.7	3.7	1.6	9.5	2.9	0.7	3.0	3.9	0.0	7.7	0.2	
292	12	47.9	5.0	1.4	15.2	0.0*	1.3	2.6	4.7	0.0	8.5	0.2	
Inviolate	1550	12	147.7	15.0	21.4	31.5	0.0*	2.2	4.3	7.0	0.0	13.5	1.1

† Signifies stand thinned.

* At age 12 branch wood includes bark.

PERCENTAGE OF ABOVE-GROUND DRY MATTER IN STEM

TAHI	34	42	36	39	41/55	59	58	54	58/58	57	62
RUA	39	39	42	42	40	59/67	66	65	65	64	63
TORU	36	44	41	41	43	53	61/68	65	65	64/64	68
INVIOULATE											71

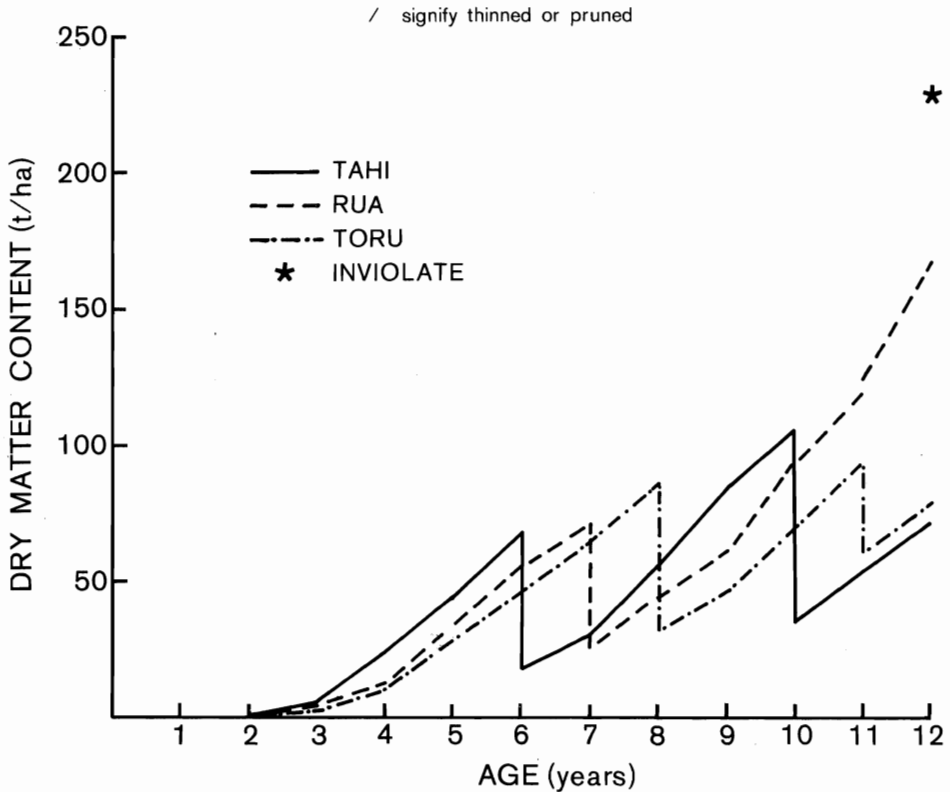


FIG. 4—Above-ground dry matter content (t/ha) of live trees at Puruki.

A comparison of stand weight and error estimates by three estimation methods is given in Table 6. (Error includes sample tree error but excludes between-plot basal area error which is not relevant for the purpose of developing estimates of dry matter partitioning among above-ground components). The weight and error estimates were very consistent between the three prediction methods used in spite of inadequate sample numbers for reliable estimates of precision using the ratio of means method (Cochran 1963).

TABLE 6—Comparison of leaf, branch, and stem weight (t/ha) and error estimates (% of mean) by commonly used prediction methods at age 6 (1979) and age 12 (1985) (H.A.I. Madgwick, pers. comm.)

Stand/method	Leaf		Branch		Stem	
	Wt	SE%	Wt	SE%	Wt	SE%
Puruki (age 6)						
Log-log	13.4	5	16.5	5	23.2	5
DSQ	14.7	—	18.1	—	23.2	—
BA ratio	14.7	5	18.2	6	23.4	5
Tahi (age 12)						
Log-log	6.8	9	19.0	10	42.6	9
DSQ	6.9	—	18.8	—	42.8	—
BA ratio	7.0	8	18.6	8	44.8	8
Rua (age 12)						
Log-log	13.2	8	43.8	8	103.7	7
DSQ	13.3	—	44.9	—	105.1	—
BA ratio	13.2	7	43.9	8	105.1	7
Toru (age 12)						
Log-log	8.9	7	15.5	7	52.1	7
DSQ	8.5	—	15.2	—	52.9	—
BA ratio	8.5	6	15.2	6	52.9	6

Method:

- (1) Log-log is linear regression of natural logarithm weight against natural logarithm dbh.
- (2) DSQ is linear regression of weight against dbh squared. Error was not calculated as variance was not homogeneous.
- (3) BA ratio is the ratio of mean weight to mean basal area.

Mortality

No branch mortality was evident in the inviolate plots until 1979, when mortality increased rapidly to almost 6 t/ha/year from 1981 onwards. Tree mortality increased from 1981 (Fig. 2), following a decline in the height growth of the shorter trees and a rapid rise in the base of the green crown of more vigorous neighbours (Fig. 3). This sequence of events indicates that the smaller trees are being suppressed due to competition for light.

Limited branch mortality had occurred in Tahi, Rua, and Toru prior to the first thinning (Table 5). Branch mortality occurred again in Rua and Toru in 1983 and 1984, respectively, indicating canopy closure for the second time. Thinning in Tahi prevented further branch mortality.

Adjustments to production estimates to account for mortality were small in thinned stands.

Leaf Area (All Surfaces) Index Over Time

Leaf area index (LAI) (Table 7) peaked at age 6 and was highest for Tahi and lowest for Toru. Leaf area index declined with stand age, largely parallelling the changes in foliage weight. Canopy specific leaf area at Puruki has been examined by Beets & Lane (1987).

TABLE 7—Leaf area index (all surfaces) of *Pinus radiata* stands at Puruki measured annually from ages 2 to 12 years

Stand	Age (years)	Leaves >2 yr	Leaves 2 yr	Leaves 1 yr	Leaves immature	Leaves total
Tahi	2	0.1	0.3	0.9	0.5	1.8
	3	0.0	0.4	3.6	0.2	4.2
	4	0.0	2.1	11.7	0.2	14.0
	5	0.1	5.0	15.0	0.1	20.1
	6	4.2	9.4	19.5	0.0	31.1
	^T 6	0.4	0.9	5.4	0.0	6.8
	7	0.0	1.7	6.2	0.2	8.1
	8	0.3	3.6	10.5	0.1	14.4
	9	0.6	5.7	11.0	0.2	17.5
	10	0.5	6.9	10.8	0.0	18.2
	^T 10	0.2	2.3	3.6	0.0	6.1
	11	0.8	1.9	3.4	0.0	6.2
12	0.7	2.3	7.5	0.0	10.6	
Rua	2	0.0	0.1	0.4	0.3	0.9
	3	0.0	0.0	3.4	0.3	3.7
	4	0.0	0.9	6.7	0.1	7.6
	5	0.4	6.3	11.8	0.0	18.4
	6	3.2	9.5	13.6	0.0	26.3
	7	0.0	5.0	11.6	0.2	16.8
	^T 7	0.0	1.5	3.7	0.1	5.4
	8	0.1	1.3	7.5	0.2	9.0
	9	0.0	1.3	9.9	0.1	11.3
	10	0.0	4.8	10.2	0.0	15.0
	11	2.8	5.6	6.4	0.0	14.8
	11	2.9	5.8	6.6	0.0	15.3
12	4.6	5.3	9.6	0.0	19.5	
Toru	2	0.0	0.1	0.4	0.2	0.6
	3	0.0	0.0	1.5	0.1	1.6
	4	0.0	0.3	6.0	0.0	6.3
	5	0.1	5.9	10.5	0.0	16.6
	6	0.1	5.5	16.5	0.0	22.1
	7	0.0	5.0	13.2	0.4	18.6
	8	0.2	3.9	14.4	0.2	18.7
	^T 8	0.1	0.9	6.0	0.1	7.1
	9	0.1	2.2	6.5	0.0	8.8
	10	0.3	4.8	9.4	0.0	14.5
	11	1.8	7.2	9.7	0.0	18.7
	^T 11	1.2	4.7	6.3	0.0	12.1
12	1.9	4.1	7.3	0.0	13.3	
Inviolata	12	3.4	6.3	11.1	0.0	20.8

^T Signifies stand thinned as indicated in Table 5.

Current Annual Dry Matter Production Above-ground

Above-ground production increased from 2 t/ha/year to over 40 t/ha/year (Table 8). The precision of production estimates decreased with time (Table 9), owing to the much larger variance associated with the stem production estimates. In spite of this,

TABLE 8—Current dry matter production (t/ha/year) in the subcatchments at Puruki

Stand	Component	Increment period (years and age)									
		'75-'76 2-3	'76-'77 3-4	'77-'78 4-5	'78-'79 5-6	'79-'80 6-7	'80-'81 7-8	'81-'82 8-9	'82-'83 9-10	'83-'84 10-11	'84-'85 11-12
Tahi	Leaves	2.0	6.7	9.4	10.1	3.6	6.0	7.1	6.6	2.5	4.8
	Branches	1.3	5.3	7.1	7.4	3.4	6.8	6.7	11.2	4.5	4.3
	Stem wood	2.0	4.8	7.7	9.3	7.7	12.4	16.8	9.2	12.6	10.0
	Stem bark	0.3	0.8	0.8	1.8	0.7	1.4	1.6	1.1	1.0	1.5
	Cones/strobili	0.0	0.0	0.0	-0.1	0.1	0.0	0.5	0.1	0.3	0.3
	Total above-ground	5.5	17.6	25.1	28.4	15.5	26.7	32.7	28.2	21.0	20.9
Rua	Leaves	2.0	3.6	6.7	7.8	6.6	4.6	6.3	6.1	4.4	6.4
	Branches	1.3	1.8	5.5	11.6	-1.7	3.9	3.8	9.9	8.3	14.5
	Stem wood	1.6	2.7	7.4	8.8	17.0	11.0	8.7	19.4	13.9	25.0
	Stem bark	0.3	0.4	0.9	1.0	1.6	0.9	1.1	2.2	1.5	1.5
	Cones/strobili	0.0	0.0	0.0	0.0	0.7	0.1	0.0	0.3	0.7	1.1
	Total above-ground	5.2	8.5	20.6	29.2	24.2	20.5	19.9	38.0	28.8	48.5
Toru	Leaves	0.9	2.9	5.9	8.5	7.3	8.2	4.4	5.9	6.1	4.7
	Branches	0.6	1.7	5.5	7.0	3.8	3.6	4.6	4.3	7.0	2.6
	Stem wood	0.9	2.2	7.0	7.2	12.4	18.1	7.4	14.7	13.2	13.2
	Stem bark	0.2	0.3	0.8	1.2	1.3	1.4	1.6	1.4	0.9	1.2
	Cones/strobili	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.1	0.2	0.0
	Total above-ground	2.5	7.1	19.3	23.8	24.8	31.3	17.9	26.4	27.4	21.7

TABLE 9—Standard error of above-ground dry matter production estimates (t/ha) also expressed as a percentage of the mean production. The percentage of variance due to leaf, branch, and stem in the 1978–79 and 1984–85 increment periods at Puruki is also given, and indicates that the stem component of the above-ground production is a large and increasing source of error

Stand	Age	SE	SE (%)	Contribution to variance above ground (%)		
				Leaf	Branch	Stem
Puruki	5–6	2.4	9	11	40	49
Tahi	11–12	5.8	27	2	15	83
Rua	11–12	11.5	24	1	21	78
Toru	11–12	5.0	23	1	8	91

Note: Variance estimates based on the basal area ratio method given in Table 6. Because branch and stem production were obtained from the change in stand weights in successive years the variance of these components enters twice, but for leaf only once.

above-ground production was correlated with leaf area index (Fig. 5). The general form of this relationship is as expected if dry matter production is linearly related to the amount of light intercepted, and the fraction of light intercepted is asymptotically related to LAI (M. G. R. Cannell, pers. comm.). For a given LAI, the amount of production tended to increase with stand age (Fig. 5). This tendency was more especially evident in the older unthinned and lightly thinned stands.

Partitioning of production amongst above-ground components varied with stand age but not with stocking (Fig. 6a, b, c). Partitioning to leaves averaged 27% over the 10-year-period but decreased from 40% in young stands to less than 20% by age 12, with stand age accounting for 78% of the variation. Partitioning to branches tended to decline at age 6 then increased again. However, the data for Rua were very variable at ages 5 and 6 (Fig. 7) but not unlike the others at age 12, suggesting that partitioning to branches was constant in all thinning treatments with age. Partitioning to stem wood plus bark averaged about 50% over the 10-year period, but increased from 35% initially to around 60% later, with stand age accounting for 46% of the variation. Stem bark remained constant at around 5% at all ages.

These partitioning changes had important effects on component dry matter relationships:

- (a) The amount of leaf production and its ability to multiply decreased with time (Fig. 7). For example, Tahi with 1-year fascicles at 2 t/ha in year t multiplied during the initial succession to canopy closure to 6.5 t/ha in year $t+1$, compared with 2.5 t/ha after the second thinning. The implications of this result on the nitrogen nutrition of the stands have been explored by Beets & Pollock (1987), and possible effects on root:shoot ratios are discussed later.
- (b) The ratio of stem to leaf production increased with age from around 1 at age 2 years to 3 at age 12 (Fig. 8). The ratio of branch to leaf production concurrently doubled. Evidently woody growth and leaf growth cannot be assumed to be in constant relationship.

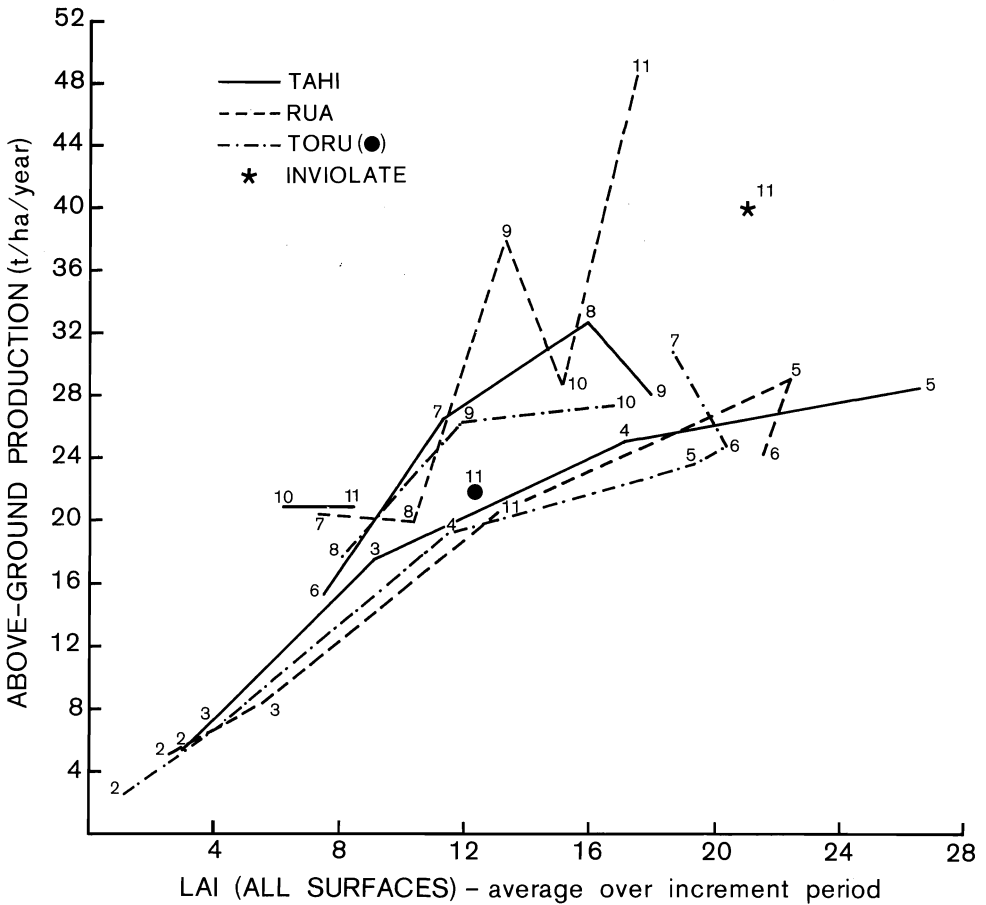


FIG. 5—Current annual dry matter production above-ground v. leaf area index (age at beginning of period indicated).

- (c) The ratio of stem production to total leaf weight or leaf area more than doubled with stand age. The use of such derived relationships is common in the literature (e.g., Binkley & Reid 1984) but is not useful without an understanding of the underlying biology.

DISCUSSION

Puruki is typical of volcanic plateau sites converted from pasture to pines in its exceptional fertility and soil moisture status (Beets & Brownlie 1987). *Pinus radiata* productivity at Puruki is very high. Based on dry matter data analysed to 1981 (Beets 1982), the stands were at the upper limit of leaf weight/stand age relationships for *P. radiata* (Madgwick 1985), total dry matter production represented at 3.7% conversion efficiency of incoming photosynthetically active radiation (Rook 1985), and the dry matter partitioning strategy above-ground was considered optimal for maximising

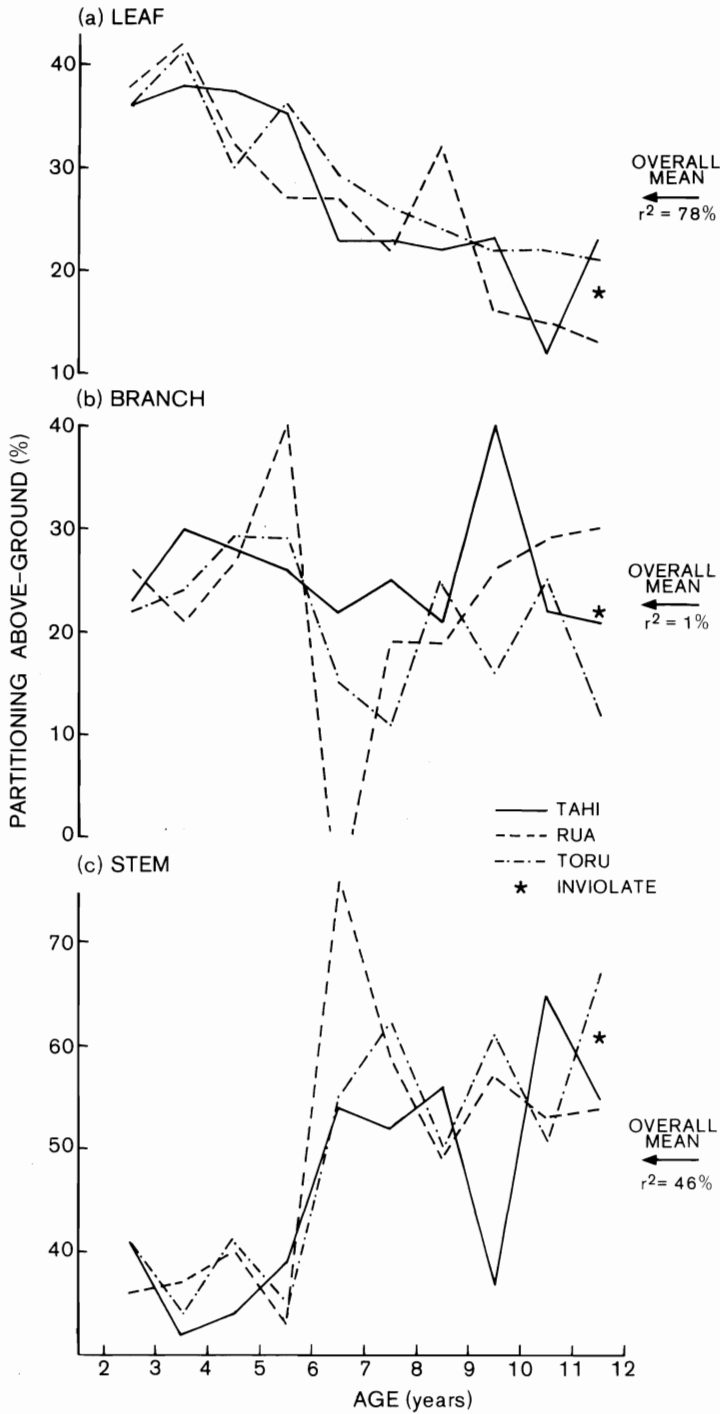


FIG. 6—Percentage of above-ground production partitioned to (a) leaves, (b) branches, (c) stems, by stand age and thinning treatment.

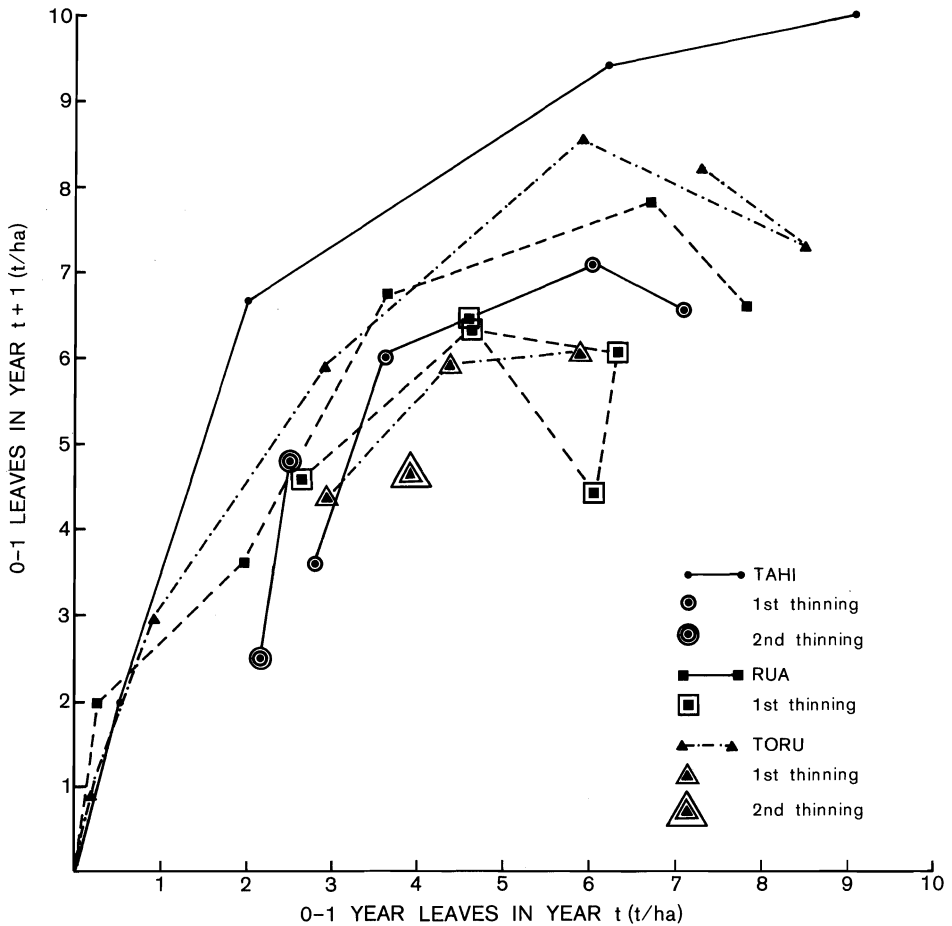


FIG. 7—Leaf production as related to previous state.

growth (McMurtrie 1985). Results to 1985 reaffirm that productivity is at the upper limit recorded worldwide, based on data by Cannell (1982) and Satoo & Madgwick (1982), though even greater stem productivity has been reported in *Eucalyptus regnans* F. Muell. stands growing in the same region and treated with fertiliser (Frederick *et al.* 1985).

The methods used provided unbiased (Madgwick 1983) estimates of plot weights within 10% and estimates of above-ground current dry matter production within 30%. Stems were estimated more precisely than leaves and branches in terms of standing crops, but the reverse applied for current production estimates – especially in older stands. Age series data based on a range of stands, the basis of most information on dry matter production and partitioning, must include a between-plot error term in addition to the sample-tree error term. Error estimates on production would then be larger, making the interpretation of such data extremely difficult. The error on the

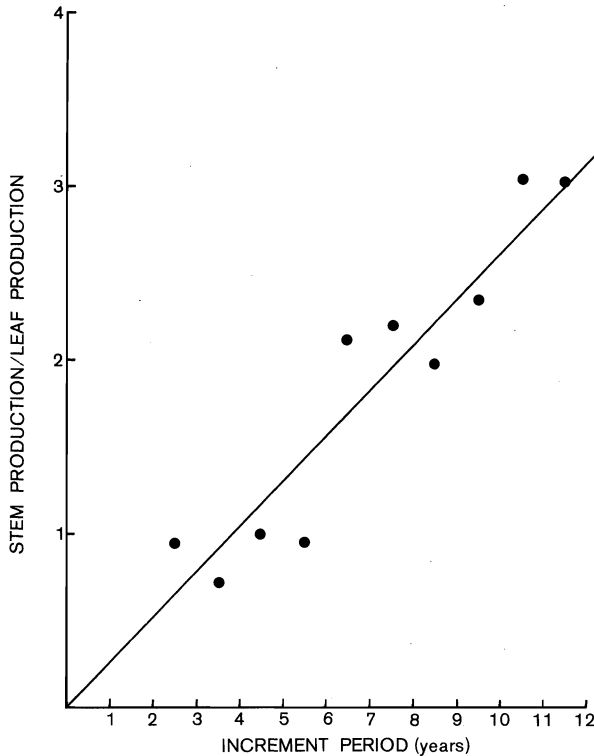


FIG. 8—Relationship between stand age and the ratio of stem to leaf production averaged across subcatchments.

current dry matter production estimates reported here includes only that associated with the relatively small number of sample trees included in the ratio estimators. Because the biomass procedures provided accurate individual tree data, the magnitude of the error reflects real differences in component relationships, suggesting the possible importance of tree-to-tree variability in partitioning. Trends in these data are, therefore, the main focus of attention in assessing the effects of age and thinning, as these are based on the full set of sample trees.

Partitioning of dry matter production above-ground was clearly related to stand age, with a large investment in leaves initially, followed by a greater investment in stem wood later. The trends in Fig. 6a and 6c suggest further changes in partitioning to leaves and stem are likely as the stands age beyond 12 years. As 4 t leaf production/ha may be expected at age 30–40 based on many studies summarised by Madgwick (1985), partitioning to leaves could decrease to around 10% at Puruki by the end of the rotation.

The stands did not return to the juvenile partitioning strategy after thinning. Instead, partitioning in the thinned stands remained similar to that in the unthinned stand at age 12, in spite of large differences in tree sizes. Stocking effects may become evident

later at Puruki as partitioning to leaves and branches declined more markedly with age at the much higher stocking reported by Madgwick & Oliver (1985), even though the early production data were similar to those from Puruki. The evidence for reduced partitioning to branches at very high stockings seems conclusive but branches were poorly estimated in most studies (Satoo & Madgwick 1982; Cannell 1985).

The question of why the efficiency of dry matter production above-ground, at a given LAI, increased with stand age is perplexing, given the increase in average leaf age and the expectation that respiratory costs will increase as biomass accumulates. A reduction in partitioning to roots, rather than an enhanced photosynthetic efficiency, may be involved (Linder & Rook 1984), as the improved efficiency occurred regardless of whether the canopy was open or closed. Stem wood benefited most from the increased production above-ground, contributing at least in part to the decrease in partitioning to leaves in older stands. Clearly, it is desirable to express partitioning on a total dry matter production basis, though if the possible effects of differential respiration rates with time and tissue type are to be considered, photosynthates available for growth and maintenance are the appropriate basis.

Root production was determined at age 12, allowing partitioning to be expressed on a total dry matter production basis at that age, and inferences to be made at younger ages. Fine root production was 2 t/ha/year in both Tahi and Rua, based on coring techniques for monitoring standing crops of live and dead roots and root decomposition (Santantonio & Santantonio 1987). Coarse root (> 5 mm diameter) standing crops in Rua were 31.1 and 36.8 t/ha in 1984 and 1985, respectively, using the coarse root prediction equation of Jackson & Chittenden (1981) applied to our plot dbh data. The comparable estimates for Tahi were 13.4 and 19.7 t/ha. Root production was therefore around 8 t/ha/year in both Rua and Tahi, and total production around 47 and 29 t/ha/year, respectively. Assuming total production in the Rua stand was constant while the canopy was closed, it was estimated that roots, which received only about 20% of the production at age 12, would have had to receive 50% of the total production at age 6 – this increased partitioning to roots to account for the difference in above-ground production observed at those ages. Tahi, an open stand, partitioned approximately 30% to roots at age 12 but 50% at age 6, at equivalent leaf areas, by the same method of calculation. If the greater above-ground productivity of the older stands is due to a reduction in partitioning to roots, further changes are likely to be small given the low investment in root growth at age 12.

Given the assumptions and limitations of the data, the effect of stand age and thinning on partitioning of total dry matter production in young stands of *P. radiata* growing without water or nutrient limitations can be summarised as follows:

- (a) Partitioning to leaves and fine roots decreases with age irrespective of thinning;
- (b) Partitioning to branches, stem bark, and stem wood increases with age;
- (c) A shift from stem wood to structural roots is a transient response to thinning;
- (d) A shift from both fine and structural roots to stem wood may be the most important age-related change in partitioning of production in closed canopy stands.

These partitioning changes are supported by the following information from Puruki and elsewhere. A reduction in leaf growth would normally be expected to signify a

restriction in nutrient supply (as is evident from numerous fertiliser studies involving nitrogen — *see* Beets & Madgwick *in press*), but at Puruki nutrient limitation can be discounted for two reasons based on the growth of the trees. The reduced absolute and relative levels of leaf growth observed by age 12 coincide with (1) a very low investment in fine roots — signifying favourable nutrition (Keyes & Grier 1981; Linder & Axelsson 1982), though some dissension occurs on this point (Nadelhoffer *et al.* 1985). However, given also (2) that in closed canopy stands dry matter production above-ground at age 12 is greater than occurred at any previous age, there seems little room for further controversy. Furthermore, the soil and foliar analysis data indicate ample supplies of nutrients for *P. radiata* growth (Beets & Brownlie 1987).

The expected decline in partitioning of growth to roots with age is consistent with the hypothesis that a functional equilibrium is maintained (*see* Thornley 1972 and Reynolds & Thornley 1982 for mathematical representations) between the size and activity of the root and shoot systems. When the Puruki nitrogen uptake data (Beets & Pollock 1987) are expressed on an above-ground dry matter production basis, shoot nitrogen demands upon the root system evidently decrease over time (Fig. 9). This decrease is significant because nitrogen is the nutrient required in greatest amounts (Madgwick *et al.* 1977) by *P. radiata* and therefore the nutrient most likely to influence partitioning. The hypothesis requires a reduction in fine roots (which are functionally

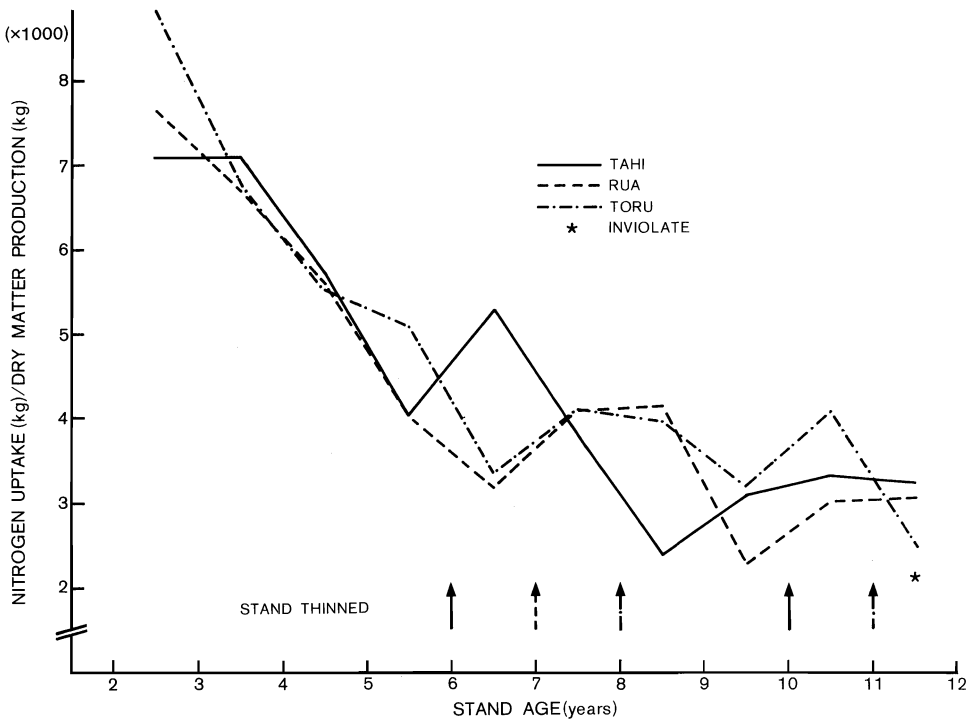


FIG. 9—Annual nitrogen uptake (kg) per unit of dry matter production above-ground (kg) at different ages.

important for nutrient uptake) with age if the specific root activity remains constant or increases – a decrease in specific root activity at Puruki is unlikely because competition with weeds for nutrients was more intense at younger ages (Beets & Pollock 1987). Furthermore, the absence of a clear thinning response (Fig. 9) means that, by the functional equilibrium hypothesis, partitioning need not increase to fine roots after thinning, which is consistent with the finding of Santantonio & Santantonio (1987) who showed that fine root growth at age 12 was a constant percentage of the total production irrespective of thinning treatments.

Structural root growth declines with age although it increases transiently after thinning, as was evident by applying the general equation from Jackson & Chittenden (1981) to our plot tree dbh data. Structural root growth accounts for 12% and 22% of total dry matter production in Rua and Tahi, respectively, at age 12, exceeding that for fine roots which averages around 5% in both stands. These predictions for structural roots are in accord with the findings of Jacobs (1939), who reported a downward shift in the distribution of stem growth after thinning – preventable by staying the trees.

Results from experiments with cuttings (rooted twigs) of *P. radiata* are consistent with the age trends given above but physiological rather than chronological age may be important. For example, cuttings from older parent material have a reduced ability to root and also seem to produce leaves more slowly compared to cuttings from younger parents (Menzies & Klomp 1987). The effect of maturation on the early height and diameter growth rates of grafts and cuttings and comparison with seedlings are well known (Sweet 1973; Sweet & Wells 1974). Furthermore, tree-origin cuttings accumulate significantly more dry matter above-ground, on a unit leaf weight basis, than hedge-origin cuttings (Hood & Libby 1978). The suggestion that hedging influences the morphogenetic development of cuttings seems to be a well-established fact (Bolstad & Libby 1982). Climate may also be involved in tree aging (Menzies & Klomp 1987) and rooting (Cameron & Rook 1974). The effects of age on partitioning should therefore be considered in terms of physiological age when generalising the Puruki results.

CONCLUSIONS AND IMPLICATIONS

In sites without major water or nutrient limitations to the growth of *P. radiata*:

- (1) Partitioning changes occurred throughout the first 12 years of stand development. On an above-ground basis, partitioning to leaves decreased, stems increased, and branches and stem bark remained constant with increasing stand age;
- (2) Partitioning was not influenced by thinning in spite of the large differences in tree size induced by this management operation;
- (3) Above-ground dry matter production for a given LAI increased with stand age. A shift in partitioning from roots to stems was probably involved, rather than an increase in the efficiency of production *per se*. Hence, large errors can be incurred by relating above-ground production directly to intercepted radiation; total production should be used;
- (4) These partitioning changes reduce the capacity of the canopy to increase after thinning, but at the same time partially offset the effect of thinning on stem production;

- (5) The reduction in partitioning to leaves, the expected decline to fine roots, and the increase to stem with increasing age underlie and explain the behaviour of cuttings originating from different-aged parent trees;
- (6) Physiological age rather than chronological age may be a worthwhile concept in generalising results from Puruki to other areas.

ACKNOWLEDGMENTS

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