Demography of the long-lived conifer *Agathis ovata* in maquis and rainforest, New Caledonia

Enright, N.J.[1*]; Miller, B.P.[1] & Perry, G.L.W.[2]

[1]*School of Anthropology, Geography and Environmental Studies, The University of Melbourne, Parkville, Australia 3010;* [2]*Department of Geography, King's College London, Strand, London WC2R 2LS, UK;* [*]*Corresponding author; Fax +61383444972; E-mail neal@unimelb.edu.au*

Abstract. The endemic New Caledonian conifer *Agathis ovata* occurs as an emergent tree in fire-prone shrublands (maquis), and fire-sensitive rainforest. Growth, survivorship and recruitment over 5 yr were compared for populations from forest and maquis on ultramafic substrates in New Caledonia to investigate whether demographic behaviour varied in response to the strongly contrasting forest and shrubland environments.

Growth of seedlings and of small (30-100 cm height) and large (100 cm height; 5 cm DBH) saplings was slow, but varied significantly among stages, site types and years. The greatest difference in growth rates was among stages, seedlings growing 0.34 cm.yr^{-1}, small saplings 1.06 cm.yr^{-1} and large saplings 2.13 cm.yr^{-1}. Tree DBH increased by only 0.05 cm.yr^{-1} and, based on these rates, individuals with DBH of 30 cm are estimated to be more than 700 yr old. Few trees (3.5%) produced cones in any year and seedling recruitment was low, but some recruitment was recorded each year in both maquis and forest. Rates of recruitment per parent were highest in forest (1.28.yr^{-1}, cf 0.78.yr^{-1}), but the higher density of trees in maquis meant that overall recruitment was greater there (92 ha^{-1}.yr^{-1}, cf 56 ha^{-1}.yr^{-1}). Seedling mortality ranged from 0.9 to 2.9% among years with no significant difference between maquis and forest. No sapling mortality was recorded, but annual tree mortality ranged from 0 to 1.4%. Evidence from a recently burned site indicated that while trees may survive fire, seedlings and saplings do not. Post-fire seedling recruitment per ha from surviving trees was four times lower than in unburned sites, but growth rates were four times higher.

Similar demographic attributes, including high survivorship, low growth rate and low rates of recruitment over a long reproductive life, characterize *Agathis ovata* populations in both maquis and rainforest in New Caledonia and are indicative of a broad tolerance of light environments that is unusual among tree species. These demographic attributes help to explain the long-term persistence of the species in these strongly contrasting habitats.

Keywords: Fecundity; Growth; Maquis; Rainforest; Survivorship.

Abbreviations: CEC = Cation exchange capacity; NDF = neighbourhood density function.

Introduction

A light/moisture trade-off is hypothesized for tree species such that shade tolerance and drought resistance should be negatively correlated (Barton 1993). According to this trade-off, few tree species that establish in closed forest sites would also be expected to establish readily in open habitats (and *vice versa*), since there will be changes in competitiveness along the resource gradient from closed forest to open vegetation. Most forest tree species that are also found in open sites are characterized by drought resistance, shade intolerance and limited evidence of recruitment under closed forest conditions, and are regarded as only secondary components of closed forests (e.g. many oak and pine species of North American forests and woodlands; Abrams 1996). Their presence in forest is maintained primarily through recurrent, but typically infrequent, landscape scale disturbances (e.g. fire or storm), that initiate secondary successions within which they may exhibit early dominance, and through long-term persistence due to great longevity (Ogden 1985; Enright et al. 1999).

The conifer, *Agathis ovata*, occurs as an emergent tree, 8-15 m in height, in high diversity, open shrublands (maquis) 1-2 m tall, and as a canopy emergent (to 25 m) in angiosperm-dominated (closed) rainforests in New Caledonia (Plate 1). No angiosperm trees in New Caledonia, and few other conifers, occur as dominants under such strongly contrasting habitat conditions. The structural formation of large, long-lived trees scattered through a fire-prone, high diversity shrubland is unusual and their dynamics are not fully understood (Jaffré 1995). In the juvenile stages, individuals in maquis are subjected to the stresses of high light and high temperature and disturbance by fire, while in forest they grow in a moist, shaded environment (McCoy et al. 1999; Enright et al. 1999) with disturbance most likely to occur through occasional tree-falls. Enright & Goldblum (1998) described stand size structures for *A. ovata* populations across a range of sites from closed forest to open maquis,

reporting the presence of seedlings and saplings in all habitat types, but with sapling densities consistently highest in maquis. Based on tree-ring counts and limited growth rate data for trees only, they estimated trees in maquis were up to 400 yr old and identified branching patterns as reflecting growth in an open environment. This was interpreted to indicate that the 'Agathis in maquis' community pre-dates European impacts (< 200 yr) on the New Caledonian vegetation and either may relate to Melanesian impacts on vegetation over a period of up to 3000 yr of human history (Enright & Gosden 1992), or a pre-human occupation ('natural') ecology. However, no data were available on recruitment, growth and survivorship to reveal whether the species is transient (i.e. continuous recruitment is absent) in one or other of these habitat types, and to what extent disturbance influences the nature of these communities.

In this paper we compare growth, survivorship and recruitment in *A. ovata* over five consecutive years for the same maquis and forest sites used by Enright & Goldblum (1998). We hypothesize that rates of recruitment of seedlings, and growth and survivorship of seedlings and saplings, are lower in forest than in maquis. This would accord with the view that the species is an early successional element of rainforest sites that is dependent on large scale disturbance (e.g. fire) to maintain a presence in such communities. Enright et al. (1999) propose this as a general model for the demographic behaviour of members of the *Araucariaceae* of the western Pacific region. Evidence of continuous recruitment in both rainforest and maquis would indicate an extremely broad tolerance of light, moisture and temperature regimes that does not accord with current ideas on light/moisture trade-offs in trees (Barton 1993).

Plate 1. Mature *Agathis ovata* over maquis at 870 m altitude, Mt Dzumac, New Caledonia.

Study area and species

New Caledonia is located in the southwest Pacific at 20°-22.5° S and 164°-167° E (Fig. 1). The climate is subtropical, with annual precipitation ranging from < 1000 mm along parts of the (leeward) west coast of the main island to > 4000 mm at high elevations and on the windward eastern coast. Mean daily temperatures for Nouméa range from 26.2 °C in February to 19.9 °C in August (pers. comm. Metéo France, Nouméa). The southern quarter of the main island, and some isolated outcrops elsewhere, are composed of ultramafic parent materials. Soils derived from these substrates are generally low in nitrogen, phosphorus, potassium and calcium, but high in iron, magnesium, chromium, nickel, cobalt and manganese (Jaffré 1980).

Agathis ovata (*Araucariaceae*) is one of 43 endemic conifers in New Caledonia (de Laubenfels 1972; Enright & Hill 1995), 36 of which are identified by Farjon et al. (1993) as of conservation concern. Five species of *Agathis*, all endemic, are found in New Caledonia (de Laubenfels 1972). Plant communities that contain *A. ovata* include *Nothofagus* dominated and mixed species rainforests and fire-prone shrublands (known locally as 'maquis miniers'). The mixed rainforests contain a variety of angiosperm and conifer species, several of the latter (*Araucaria* and *Agathis* spp.) occurring as emergents. The maquis is comprised largely of shrubs and sedges, overtopped by an open tree layer of *A. ovata* in some places (Jaffré 1995).

Sampled populations of *A. ovata* reported here are from three areas, all on ultramafic soils in the southern part of the main island (Fig. 1) and are located at a range of altitudes: Goro plateau - Plaine des Lacs (22° 14' S; 166° 57' E; 350 m a.s.l.), Col de Yaté (22° 10' S; 166° 53' E; 400 m a.s.l.) and Mt. Dzumac (22° 3' S; 166° 26' E; 870 m a.s.l.). Climate data are limited for these locations; two years of rainfall records at Mt. Dzumac recorded annual totals of 1816 mm and 2742 mm, while 35 years of records for Ouenarou (170 m a.s.l.), 15-20 km west of the Col de Yaté and Goro sites, revealed a mean annual rainfall of 2389 mm, approximately half of which falls in the four wettest months from December to March (pers. comm. Metéo France, Nouméa).

Soils in all sites were acidic, pH ca. 3.9 in forest and 4.7 in maquis. Forest soils were much higher in %C (30.6 ± 10.4) and cation exchange capacity (CEC 15.7 ± 4.7 meq.100-g^{-1}) than maquis soils (%C 2.8 ± 0.4 and CEC 5.8 ± 0.7), reflecting the presence of distinct litter and humus layers in the forest plots. There was no difference in measured soil properties between low and high altitude maquis sites (N. Enright unpubl. data).
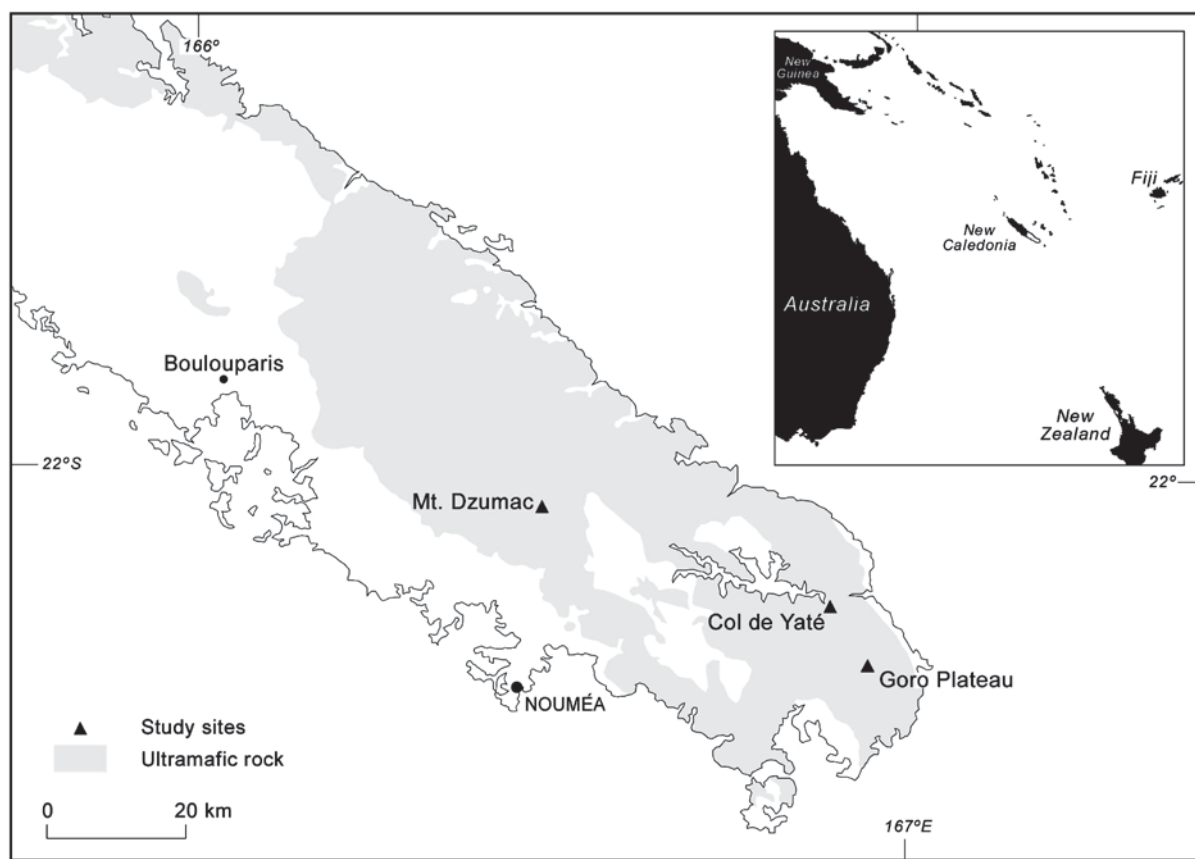
Fig. 1. Location of New Caledonia (inset) and of the three study areas at Mt Dzumac (high altitude forest and maquis sites), Col de Yaté (low altitude forest and maquis sites), and Goro Plateau (low altitude forest and maquis sites). Shading indicates the distribution of ultramafic parent materials.

Methods

Field and laboratory

Sample plots (*n* = 13) were established to trace growth, survivorship and recruitment, spanning sites ranging from open maquis on lateritic boulder fields ('cuirasse') to closed maquis and rainforest, and were censused annually from 1996 to 2001. All *A. ovata* individuals ≥ 5 cm DBH within plots of 0.125 - 0.5 ha (50 m × 25 m to 100 m × 50 m, depending on extent and density of local populations), were tagged with a numbered aluminium label, and their x-y co-ordinate position within plots was mapped to the nearest 0.1 m. DBH was measured each year, while height to the lowest branch (with a diameter >5cm) and its basal diameter was measured on one occasion. To increase the sample size for large individuals, tree samples included outlying individuals up to 50 m from the edge of plots. All saplings (≥ 30 cm height to < 5 cm DBH) in each plot were tagged and mapped. Height was measured to the apical growth tip and DBH was recorded for saplings > 1.4 m tall. Seed-

lings (< 30 cm height) were tagged for two to four randomly located 100-m² subplots per plot and height was measured as described for saplings.

Preliminary screening of data for forest plots (*n* = 5), maquis plots at low altitude locations at Yaté and Goro (*n* = 4) and high altitude locations at Mt Dzumac (*n* = 4) showed few differences in measured parameters among plots, so for analysis purposes data were grouped into three 'site types': forest, low altitude maquis and high altitude maquis. The two maquis sites are geographically (Fig. 1), as well as altitudinally, distinct. A further plot (0.25 ha) sampled a small population of *A. ovata* in a low altitude valley maquis/rainforest mosaic patch at Goro, which had been burned by a fire in November 1991. It is treated separately here so that post-fire growth, survivorship and recruitment could be compared with rates measured for the other sites.

To count cones, tree canopies were scanned each year using binoculars. Reproductive status of trees was determined either by the presence of cones or of cone scars. Canopies of forest trees were not visible for enumeration of cones, so results reflect maquis values

only. Low rates of cone set in all years mean that sample sizes were low and results for seed production and germination must be regarded as preliminary. Mean number of firm and viable seeds per cone was assessed for a sample of five cones collected from three individuals in low altitude maquis in 1997 and 1998; 40 firm seeds, collected in 1997, were tested for germination at 20 ºC in an incubator. Seedling plots were searched annually for new recruits, which were tagged and their heights and survivorship followed in subsequent years.

Hemispherical canopy photographs were used to characterize the light environment in maquis and in the forest understorey. Photographs were taken using a 180° field of view fish-eye lens 1 m above ground for five random *A. ovata* sapling and five random non sapling locations in each of three forest stands. Ten hemispherical photographs were taken in maquis.

Numerical analysis

Mean age of plants at the upper boundary of each size class was estimated using the mean growth rate (height and diameter) of plants in each size class range. Seedlings (new recruits) are ca. 8 cm high at the cotyledon stage and estimates of time to reach sapling size (30 cm) took this into account. To test for significance of difference in demographic rates between sites and years Pearson's χ^2, Likelihood ratio χ^2, ANOVA and regression analysis (Anon. 2000) were used, with transformations to meet normality assumptions as appropriate. Error terms are reported as standard error (s.e.).

The neighbourhood density function (NDF) described by Condit et al. (2000) was used in both univariate and bivariate form to investigate the spatial pattern of saplings (in plots where $n > 50$), to determine if recruits were aggregated (univariate) or associated with adults (bivariate), and if faster growing saplings (vs. slow growers) were located in a manner that might reflect within plot habitat variations in growing conditions (bivariate). Fast growers were defined as those saplings growing more than the median (ca. 2 cm) in a given year. Weighted edge corrections, based on those of Goreaud & Pelissier (1999) for Ripley's *K*, were adapted for the NDF. An Excel add in to perform this analysis (and other spatial statistics) is available by request from george.perry@kcl.ac.uk. We calculated the NDF for 0.5 m width annuli up to 12.5 m, half

the width of the plot, and 99% confidence intervals through a Monte Carlo process. NDF tests were performed for all combinations described above, together with bivariate tests for both fast and slow growing saplings against trees separately for each of the 5 yr, and for the 5-yr means. As little additional information was returned from this array of tests relative to the 5 yr mean tests, only these last results are presented here.

Percentage canopy openness was calculated for each hemispherical canopy photograph using the software package Winphot, version 5.0 (ter Steege 1994). Differences between means were tested among the three forest plots, and between sapling and non sapling locations, using one-way ANOVA and t-test for arc-sine transformed percentage data.

Results

Growth rate and estimated age

Differences in growth rate were significant across stages, sites and years and interactions among these factors were also significant (Table 1). The largest difference in growth rate was due to plant size; mean growth in seedlings (< 30 cm) was 0.34 cm.yr^{-1}, three times higher in small saplings (30-100 cm) and doubled again to 2.13 cm.yr^{-1} for large saplings (> 100 cm height). Growth rates were lowest in low altitude maquis in all three stages but were highest in forests for seedlings and large saplings, and in high altitude maquis for small saplings (Table 2). Annual variation was stronger than variation due to site and was strongest in large saplings, where mean growth varied more than two-fold from 1.27 cm.yr^{-1} in 2000-2001 to 3.24 cm.yr^{-1} in 1996-1997 (Fig. 2).

The mean percentage of the 5 yr total height growth for saplings that occurred in each year (between 1996 and 2001) ranged from 8 to 30% (Fig. 3). Generally,

Table 1. ANOVA of height growth rate per yr by stage (seedling, small and large sapling), site (forest, high and low altitude maquis) and year (1996/7-2000/01) for *Agathis ovata* in forest and maquis on ultramafic soils, Province Sud, New Caledonia.

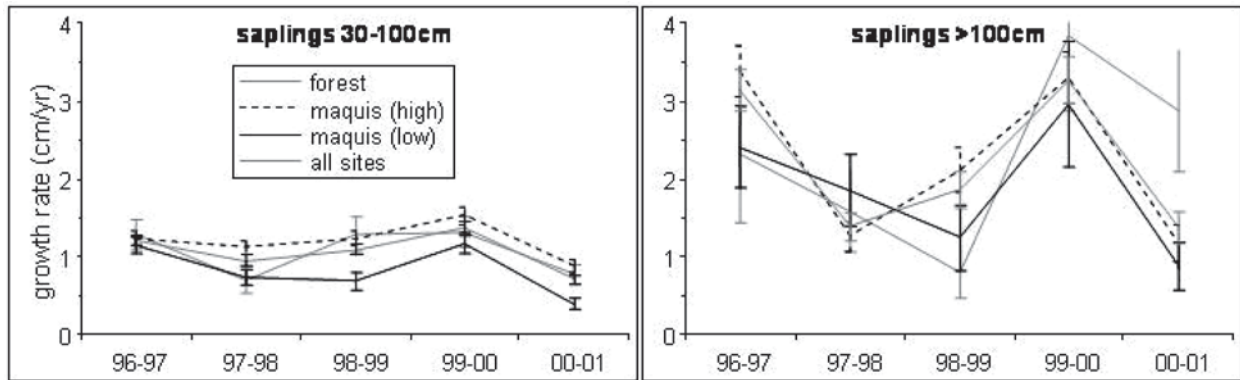| Source	df	*F*-ratio	*P*
Year	4	27.764	0.000
Site	2	9.720	0.000
Stage	2	194.507	0.000
Year × site	8	3.317	0.001
Year × stage	8	7.999	0.000
Site × stage	4	2.499	0.041
Year × site × stage	16	2.454	0.001
Error	6598		

Fig. 2. Mean stem height growth rates for *A. ovata* saplings (30-100 cm height and > 100 cm height) by year. Error bars are ± 1 s.e.

1996-1997 was the year of greatest height growth, and 1998-1999 was the year of lowest growth in forest, while 1996-1997 and 2000-2001 were respectively the best and worst years for growth in maquis. However, mean growth per year masks the year to year variations in growth among individual plants: on an individual basis, ca. 60% of total height growth occurred in just one year regardless of site type and almost 90% of total height growth took place in just two years. Only one sapling (from $n = 627$) grew ≥ 2 cm.yr^{-1} in all five years, while 1% and 8% of saplings grew by more than this amount in four and three years, respectively.

Mean tree (DBH > 5 cm) diameter growth across all sites and years was 0.49 ± 0.06 mm.yr^{-1}. Due to the extremely small changes in DBH from year to year (often within measurement error), DBH growth rate is presented only for the total increase over the 5-yr measurement period. Regression of DBH growth against DBH indicated no significant effect of stem size on growth rate ($p > 0.50$, $R^2 = 0.004$, $n = 111$). Between site differences in DBH increase were not significant after variation among plots within sites had been accounted for (nested ANOVA, $F_{2,8} = 2.30$, $p = 0.163$). In general, forest growth rates were among the lowest observed, and high altitude maquis were among the highest (0.7-0.8 mm.yr^{-1}).

Based on mean growth rates, the plants are estimated to be very long-lived: seedlings attain a height of 30 cm after ca. 50-60 yr, require a further 65-75 yr to reach a height of 1 m and attain a DBH of 5 cm at age 230-310 yr (Table 2). Overall, mean growth rates result in an estimated age of 700 to 780 yr for trees at 30 cm DBH and trees of 100 cm DBH could be > 1500 yr old.

Reproduction, recruitment and survivorship

In maquis, where cone production could be measured, only 15 trees (3.5% of the total 374 trees surveyed) and three large saplings (1.9%) were observed to reproduce over the six years of observation. Two trees reproduced in two of six years, one reproduced four times and the remaining 11 trees reproduced just once each: a total of 20 reproductive events (Table 3). No reproduction was observed in 1996 and only one tree reproduced in each of 1997 and 1999, in each case producing one cone. The highest number of trees reproducing in any year was eight in 1998 when 2% of maquis trees produced cones. Three saplings, 200-230 cm tall and DBH 3-3.5 cm, produced one cone each. Overall, a total of 64 cones were observed over six years, with 75% of these cones produced by just four trees. Reproductive individuals did not differ from the mean in their growth rates. One reproducing tree and one sapling were from the high altitude maquis and the remainder were from the low

Table 2. Five-yr mean annual stem height growth (cm.yr^{-1} ± s.e.) of seedling and sapling sized plants and estimated plant age (yr, at the upper limit of size class), of *A. ovata* in forest and high and low altitude maquis on ultramafic soils, Province Sud, New Caledonia.

| | Maquis (high) | | Forest | | Maquis (low) | |
	Growth	Age	Growth	Age	Growth	Age
Seedlings to 30 cm	0.39 ± 0.03	51	0.41 ± 0.03	55	0.36 ± 0.02	60
Saplings to 100 cm	1.20 ± 0.04	117	1.03 ± 0.08	128	0.83 ± 0.05	134
Saplings 1m ht to 5 cm DBH	2.23 ± 0.13	233	2.36 ± 0.36	309	1.61 ± 0.19	265
Trees to 30 cm DBH*		700		777		733

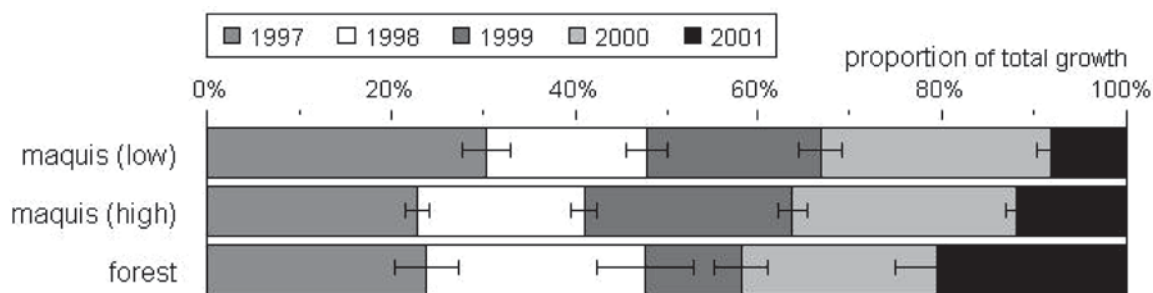* based on mean total diameter growth (pooled across all sites)

Fig. 3. Mean annual proportion of total height growth over 5 yr per *A. ovata* sapling per year from 1996-1997 to 2000-2001, by site type. Error bars are ± 1 s.e. *n* = 328, 33 and 125 for high altitude maquis, forest and low altitude maquis, respectively.

altitude maquis. Cones contained 100 to 145 cone scales and a mean of 24.4 ± 5.0 firm seeds and 23.0 ± 6.8 empty (aborted) seeds. Germination rate for the 40 firm seeds tested was 100%.

A total of 41 new recruits was encountered in seedling subplots. Recruitment was relatively uniform among years, albeit with small peaks in 1999 and 1997 (Table 4). Between site differences were strong, with mean recruits per tree lowest for the high altitude maquis (0.78) and highest (1.28) for forest. Recruits per putative parent peaked in forest at three seedling.tree^{-1} in 2000 and in low altitude maquis in 1997 at 2.4 seedling.tree^{-1}, but were consistently low for high altitude maquis (max. 1.24 in 1998). Estimated recruitment was lowest in forest at 56.ha^{-1}.yr^{-1} (± 18) with 73 ± 19 in high altitude maquis and 92 ± 33 in low altitude maquis (Table 4).

Over the 5 yr of the study, 75 plants died, 3.6% of the total number surveyed. Most of these were seedlings, in which annual mortality was ca. 2% (Table 5). The highest annual mortality rates occurred in high altitude maquis, peaking at 6.1%. No clear pattern among years was discernible for any plant size or site type: only in low altitude maquis was there a year when no seedling mortality was observed. Mortality in larger size classes was infrequent, with none observed in any year for large saplings. Small sapling mortality was 2% for high altitude maquis in 1999-2000, but was not observed elsewhere at any time. Mortality of trees in the size range 5-

30 cm DBH was observed in all site types in the last two years of the survey, but never exceeded 1%. Large tree (> 30 cm DBH) mortality was observed only for the high altitude maquis, where it reached 1.4% in 1996-1997 (Table 5). At these rates, we estimate that 30% (low altitude maquis) to 36% (high altitude maquis) of established germinants survive the 50-60 yr required to reach the sapling stage, and most (24-30% of germinants) survive to become saplings > 100 cm in height.

Canopy openness and tree growth form in forest and maquis

Mean canopy openness of forests containing *A. ovata* was 10.8 ± 0.6% of open sky. There was no difference between the three forest areas sampled (ANOVA, $F_{2,27}$ = 2.93, *p* > 0.05), nor between the canopy openness for understorey locations where saplings were growing vs. random understorey locations (*t* = − 1.92, *p* > 0.05). Maquis sites had canopy openness values ranging from 34.1% for a sapling on a sharp forest/maquis boundary on a steep south-facing slope, to > 90% for an open site with *A. ovata* trees downslope only.

Mean branching height (height above ground to first branch > 5 cm diameter) varied significantly among sites (ANOVA $F_{2,120}$ = 43.8, *P* < 0.001). Mean first branch height in forest trees was 5.1 ± 0.5 m (*n* = 38) and reached as high as 12 m. Low and high altitude maquis mean first branch heights were 1.2 ± 0.1 m and 1.8 ± 0.2

Table 3. Frequency and abundance of cone production by year for *A. ovata* trees in maquis (pooled for high and low altitude maquis sites), Province Sud, New Caledonia.

	1996	1997	1998	1999	2000	2001	1996-2001
Percentage of trees reproducing	0	0.3	2.1	0.3	1.1	1.6	4.0
No. of trees reproducing	0	1	8	1	4	6	15
Total cones produced	0	1	22	1	15	25	64
Cone production / tree	0	0.3	5.9	0.3	4.2	6.7	3.4
Cone production / reproducing tree	0	1.0	2.8	1.0	3.8	4.2	4.3
Max. cones /tree	0	1	12	1	12	10	15

Table 4. Annual, and 5 yr mean seedling recruitment ha^{-1}(1997-2001) for *A. ovata* in high and low altitude maquis, forest, and for all sites pooled, Province Sud, New Caledonia.

Year Site	1997	1998	1999	2000	2001	5-yr mean
Maquis (high)	100 ± 63	100 ± 37	83 ± 40	33 ± 33	50 ± 34	73 ± 19
Forest	0	11 ± 11	78 ± 36	133 ± 60	56	56 ± 18
Maquis (low)	183 ± 145	100 ± 52	117 ± 60	33 ± 21	25 ± 17	92 ± 33
All sites	81 ± 46	62 ± 20	90 ± 25	76 ± 29	45 ± 21	71 ± 13

m ($n = 34, 51$), respectively. First branch diameters were typically large (46 ± 3%, 72 ± 6% and 53 ± 5% of stem DBH in forest, low and high altitude maquis respectively) and differed between sites (ANOVA $F_{2,120}$ = 6.01, $P = 0.003$).

Impact of fire

Half of the 28 trees (DBH range 10-100 cm) in the post-fire plot were scorched by the November 1991 fire. Trees in the forested gully part of the plot escaped this fire, but many showed scars from at least one previous fire. All trees survived the fire, but subsequent bark swelling and shedding rendered attempts to measure annual DBH growth ineffective. Other than two saplings (40 and 60 cm height, respectively) growing in an unburned part of the plot, no saplings were recorded, and it is likely that any saplings in the burned area died during the fire.

Ten seedlings were found in the initial (June 1996) survey inside the burnt area and by the time of the 2000 survey a further 17 seedlings had been located. Some of the additional seedlings were new recruits, but others were not and apparently had been overlooked in the dense ground layer of sedges (*Lepidosperma* and *Costularia* spp.) that had grown up following the fire. Seedling growth rates were 3-4 times higher than those in the unburned sites, varying between years from 0.4 ± 0.1 to 1.6 ± 0.4 cm.yr^{-1}, mean of 1.1 ± 0.1 cm.yr^{-1}. The tallest seedling (27 cm in 2000) must have grown at > 2 cm.yr^{-1} for 8 yr, even assuming it was recruited in the first year after the fire. No tagged seedlings died and since all seedlings are post-fire recruits, the recruitment

rate at this site is estimated at 17 seedling.ha^{-1}.yr^{-1}, a value 4.2 times lower than that for the other sites.

Spatial pattern and growth

The spatial distribution of trees was not significantly different from random (i.e. homogeneous Poisson), with the exception of one plot in high altitude maquis, where trees were significantly more frequent than expected at distances of 11.5-12 m (Fig. 4). Sapling densities, on the other hand, were higher than would be expected from random distributions (Table 6), occurring in aggregations at the 0-2 m scale in all six maquis plots tested (including both low and high altitude sites). Fast and slow growing saplings showed a similar distribution as all saplings, and were neither spatially associated nor segregated. Saplings were not associated with trees at any scale in any plot, except for the high altitude maquis plot noted above, where a peak in number of saplings spaced 5-5.5 m from adults was significant.

Discussion

Evidence for differences in demographic behaviour in *A. ovata* populations between open maquis and closed forest locations, indicative of likely light and water trade-offs such as are hypothesized to operate for individuals in such strongly contrasting environments (Barton 1993), was not found in this study. Rather, this species shows high survivorship at all stages (seedling to adult), slow growth and low fecundity over a very

Table 5. Mean annual mortality (%: pooled across site types) by year and size class for *A. ovata* in forest and maquis on ultramafic soils, Province Sud, New Caledonia. n = range of n values over 5 yr.

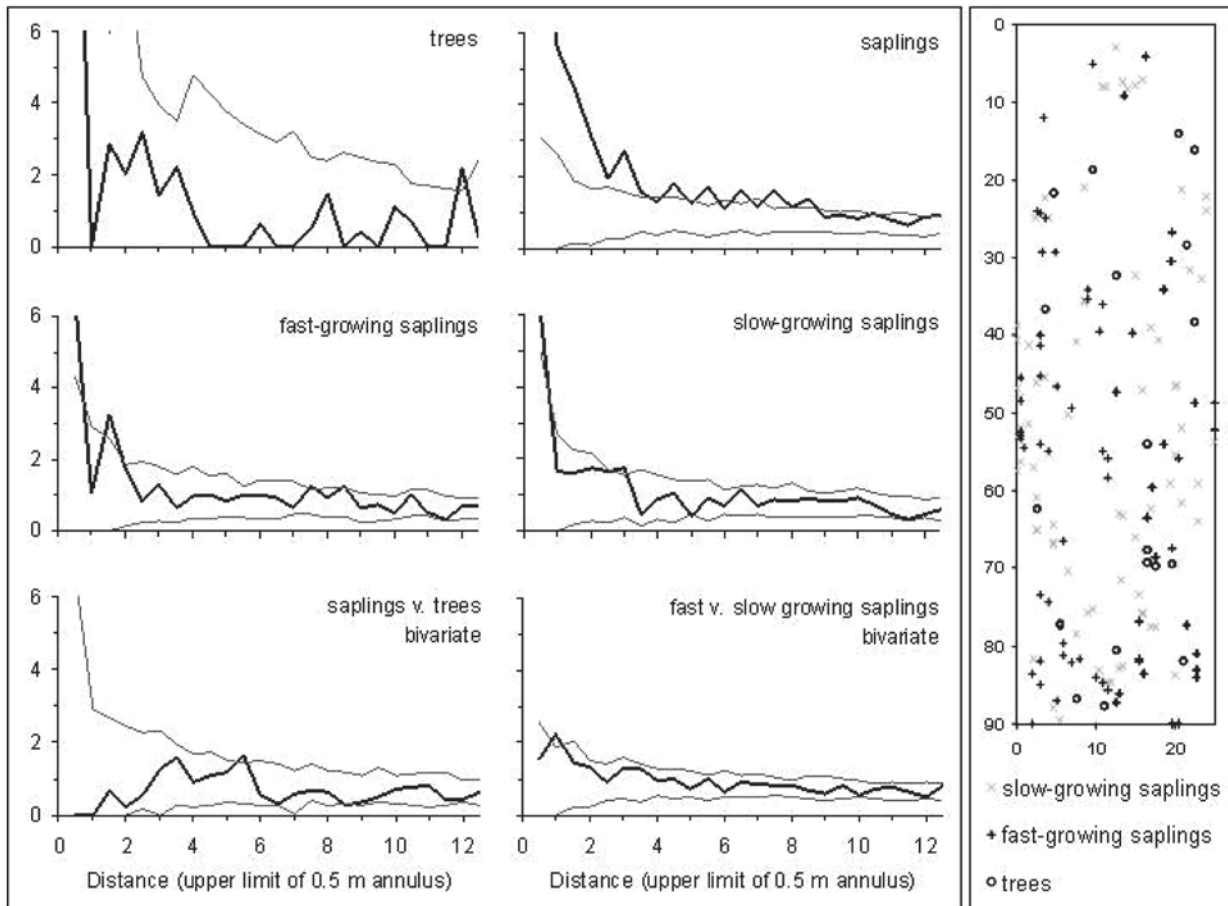| Year Size class	1996-1997	1997-1998	1998-1999	1999-2000	2000-2001	Mean	n
< 30 cm height	2.9	0.9	1.7	1.9	2.4	2.0	548-630
30-100 cm height	0.1	0.3	0.0	0.5	0.4	0.3	723-825
100 cm ht-5 cm DBH	0.0	0.0	0.0	0.0	0.0	0.0	151-200
5-30 cm DBH	0.4	0.0	0.0	1.1	0.4	0.4	270-273
> 30 cm DBH	0.6	0.0	0.0	0.0	0.0	0.1	170-172

Fig. 4. Univariate and bivariate NDF functions for *A. ovata* saplings and trees in high altitude maquis plot 1 (H1). Black lines show observed densities, grey lines indicate 99% CI's. Y-axes show density corrected NDF values. Tree and sapling locations within the plot are shown in the map on the right (axes in m).

long reproductive life regardless of sampled location and growing conditions. The absence of observable demographic differences between populations growing in communities as distinct as maquis and rainforest implies extremely high tolerance of environmental variation, and tolerance (or avoidance) of competition.

Plant height and stem diameter growth in *A. ovata* is extremely slow, both absolutely and relative to related conifers. The growth rate of seedlings is similar to that recorded for *A. macrophylla* in rainforest in the Solomon Islands, but is only half to one-third of that recorded for saplings to 1.5 m tall (Whitmore 1966). It is less than half that reported by Enright (1995) for seedlings, saplings and trees of *Araucaria cunninghamii* and *A. hunsteinii* in

Table 6. Distances (m) at which significant aggregation (univariate analyses) and association (bivariate) of *A. ovata* individuals was observed for four high altitude (plots H1 - H4) and three low altitude (plots L1 - L3) maquis sites, Province Sud, New Caledonia; ns indicates no significant pattern at any scale from 0 to 12.5 m.

Plot	H1	H2	H3	H4	L1	L2	L3
Univariate							
Trees	11.5-12	ns	ns	ns	ns	ns	ns
All saplings	0-3.5	0.5-1.0	0.5-1.0	0-5.0	0.5-1.0	0-0.5	1.0-3.0
Slow growing saplings	0-0.5	1.0-1.5	ns	0-1,2-3,4-6	1.0-1.5	0-0.5	ns
Fast growing saplings	0-0.5	2.5-3.0	0.5-1.0	1.5-2.0	1.0-1.5	0-0.5	ns
Bivariate							
Fast vs. slow saplings	0.5-1.0	0.5-1.0	ns	0-0.5, 2-6	0.5-1.0	0-0.5	ns
Saplings vs. trees	5.0-5.5	ns	ns	ns	ns	ns	ns

tropical rainforests in Papua New Guinea and by Enright & Goldblum (1998) for *A. ovata*, assuming growth rings are annual, which is based upon evidence for a number of other *Araucaria* and *Agathis* species in the western Pacific region. These studies were either of trees growing in more continuously wet tropical forests (Enright 1995; Ash 1983, 1985) or in more temperate latitudes (Ahmed & Ogden 1985). Enright (1995) and Ash (1983, 1985) found good fits between growth rate and radiocarbon estimates of tree age.

Based on tree ring widths, Enright & Goldblum (1998) calculated mean DBH growth rate for *A. ovata* of 0.14-0.22 cm.yr^{-1} and estimated maximum tree age of 400 yrs in maquis and 500 yrs in forest. Direct measurement of DBH increment here provides a mean growth rate that is 2.8-4.4 times lower, so that we now estimate an age of ca. 700 yr for trees of 30 cm DBH in both maquis and forest. The largest tree in our sample (97 cm DBH, in high altitude maquis) could be more than 1500 yrs old. Based on these new results, the small changes in DBH from year to year, relative to measured tree ring widths, suggest that no, or only partial, rings may be laid down in some years, so that tree ring counts would substantially underestimate tree age. Support for this very slow growth rate is provided by a radiocarbon date of 650 ± 100 yr (sample UWA33, unpubl.) from wood at the centre of a 33 cm DBH *Araucaria muelleri* tree with approximately 350 rings at 30 cm above the ground and growing in maquis in the same region as the low altitude maquis plots reported here.

Height growth rate for seedlings and saplings of *Agathis ovata* was greater for high altitude (850-900 m a.s.l.) maquis than for low altitude maquis (300-350 m a.s.l.). Jaffré (1995) argues that *A. ovata* is a component only of secondary maquis (successional to rainforest) at low altitudes, but is a component of both secondary and climax maquis at high altitudes. It is feasible that growing conditions for *A. ovata* may be suboptimal near the species' lower altitudinal limits in New Caledonia due to the negative impacts of higher temperatures, light and moisture stress (McCoy et al. 1999).

Despite the very large differences in likely levels of light and moisture stress between forest and maquis (Enright et al. 1999; Rigg et al. 2002), differences in growth rates for seedlings and saplings were not significant between these vegetation types. However, all but one of the forest plots was located at low altitude, so that no comparison of growth between seedlings and saplings in forest across altitudes was possible. Forests containing *A. ovata* had a mean canopy openness of ca. 10%, a value reported by Enright et al. (1993, 1999) as typical for rainforests containing *Agathis* and *Araucaria* species elsewhere in the western Pacific. They noted that these genera showed a failure of recruitment in

forests where openness was < 8%. Read et al. (1995) provide similar evidence for New Caledonian rainforests with and without *Nothofagus*, noting that recruitment in this species is absent from mature, mixed rainforests with low understorey light availability. *A. ovata* and *Nothofagus* species appear to represent early and mid successional components respectively, of developing rainforests on relatively dry microsites, with *Nothofagus* perhaps entering the succession earlier (and largely in place of *A. ovata*) in moist microsites (Read et al. 1995; Enright et al. 1999).

Many plants failed to grow in one or more years during the period of study, suggesting either that sapling height may be responding to a pattern in the environment (e.g. rainfall) or that plants require one or more years of resource accumulation between years of strong growth. Clark & Clark (1994) reported a strong, synchronized climatic effect on year to year variations in growth for six rainforest species in Costa Rica, with best growth for most species in the two driest years. They hypothesized that dry years were associated with high solar radiation levels due to lower cloud cover. In the present case, we consider that annual climatic variation is unlikely to play a significant role in determining the observed patterns of growth. Rather, vertical growth of internodes in one year may be followed by growth of lateral branches in succeeding years, or no growth, due to slow rates of resource accumulation resulting from chronic resource limitation (soil macronutrients) or stresses (photo-inhibition, drought). Rigg et al. (2002) documented high levels of photosystem II stress (using fluorometry) in seedlings and saplings of *Araucaria laubenfelsii* in maquis, but not forest, at 1000 m a.s.l. on Mt. Do, New Caledonia, implicating light stress as a possible factor limiting sapling growth in maquis. New Caledonian ultramafic soils are strongly acidic, have low CEC and generally low concentrations of plant macronutrients. Enright et al. (2001) reported low levels of P in both maquis and forest on Mt. Do, and Jaffré (1995) has shown that soils derived from ultramafic parent materials are generally deficient in N, P, K and Ca so that plant macronutrients might also limit growth.

Survivorship in *A. ovata* is high relative to most tree species, including closely related conifers. Even in the seedling class, a mean of 98% of individuals survived per year. By comparison, Enright (1995) reported mean annual survivorship of only 5.6% and 33% (each over 7 yr of measurement) for seedlings of *Araucaria cunninghamii* and *A. hunsteinii* respectively, growing in lower montane rainforests in Papua New Guinea.

Fecundity was also extremely low, with 2% or fewer trees producing cones each year, a recruitment rate of 0-3 seedling.parent^{-1}.yr^{-1} and a mean of only 24 firm and viable seeds per cone. Bowen & Whitmore (1980) found

broadly similar values for number of firm seeds per cone (5-90 seeds) for *Agathis macrophylla* in the Solomon Islands. The contrasting dynamics of *A. ovata* in New Caledonia relative to related conifers in the wet tropics elsewhere in the western Pacific is clearly illustrated through comparison with the two *Araucaria* species from New Guinea rainforests noted above. These species produce thousands of seed.tree^{-1}.yr^{-1} and recruit up to 500 seedling.tree^{-1}.yr^{-1} (Enright & Watson 1991; Enright 1995), most likely reflecting greater availability of moisture and macronutrients. While the low survivorship of seedlings in those forests means that few individuals ever become saplings, the low recruitment rate in *A. ovata* is balanced by high survivorship. In addition, the revised longevity estimated for this species means a longer reproductive life time over which recruitment might occur. This low recruitment rate is comparable to that observed in most years for another New Caledonian conifer of maquis and forest communities, *Araucaria laubenfelsii* (Rigg 1998). However, in what appears to be masting behaviour, *A. laubenfelsii* produced massive seed crops in 1995 and 2001 (L.S. Rigg unpubl. data), which resulted in very high seedling densities in those years. Although few individuals of *A. ovata* were observed with cones, these data, combined with those for new recruits found beneath other trees and occasional precocious reproduction in large saplings, suggests that most trees > 5 cm DBH are probably reproductively mature.

McCoy et al. (1999) proposed a 250 yr post-fire succession from maquis to rainforest in lowland vegetation of southern New Caledonia, with their time scale based on tree-ring counts of *Dacrydium araucarioides* and assumed annual periodicity of tree-ring production. Of 319 species in their 88 study sites, only 29 (9%) were present at all stages of the putative succession. None of these persistent species were trees and little is known of their growth rates or population dynamics. If 250 yr is accepted as the period for succession to rainforest (though we believe this to be too short; Perry & Enright 2002), it remains possible that many of these 'persistent' species may experience increasingly negative population growth with continued forest development, and eventually may be lost from the rainforest community in the absence of major disturbance. *A. ovata* provides evidence of a contrary situation. The survival of *A. ovata* trees from a fire that encroached from lowland maquis into rainforest in 1991 demonstrates the plausibility of populations surviving through fire mediated maquis and forest successional transitions. Indeed, given their estimated longevity, trees might survive several such stand level disturbances. However, the absence of smooth boled forest form trees in maquis and of low branching maquis form trees in forests provides no evidence for recent, fire mediated conversion of forest to maquis, or of succession from maquis to forest. On the contrary, it provides evidence for the long-term persistence of each community type.

While reproduction is infrequent, extreme longevity of individuals (higher than previously believed) and high survival rates across all life history stages (from seedling to adult), means that a high seedling recruitment rate is not necessary for population maintenance. In this respect the extreme longevity of *A. ovata* constitutes a significant adaptation to survival in the New Caledonian landscape where fire mediated successional processes may lead to changes from open maquis to closed forest at time scales which are shorter than the longevity of *A. ovata* individuals. The broad distribution of this species among vegetation types may reflect its ability both to persist within undisturbed stands for long periods, and to survive disturbance by fire and take advantage of post-fire changes in conditions for seedling recruitment.

Spatial pattern

Spatial pattern analysis of trees and saplings indicated random pattern in most sites at all but the smallest scale, where saplings were strongly aggregated at distances of 0-2 m. Casual observation suggests that seedlings may show greater survivorship in sedge (*Costularia* spp.) and *Xyris pancheri* (*Xyridaceae*) tussocks and in rock crevices, where decomposing organic matter and trapped rainwater maintain moist conditions in a well drained environment (Jaffré 1980). Sapling densities were never sufficiently high in any forest plot to enable the comparison of forest and maquis spatial patterns. The lack of significant aggregation among fast and slow growing saplings refutes the hypothesis that environmental heterogeneity in availability of resources, other than at the level of the individual, might explain differences in growth between saplings within plots. Despite the recent pleas of several workers for ecologists to explore the links between spatial pattern and demographic processes (e.g. Barot et al. 1999; Dale 1999), our spatial analysis results so far contribute little to our understanding of demographic behaviour in this species. There may, however, still be spatial associations due to processes as yet untested, such as the role of sedge tussocks as recruitment sites for *A. ovata*, and the abundance of such tussocks in open sites relative to sites beneath *A. ovata* tree canopies.

Conclusion

Demographic evidence presented here supports the contention that *A. ovata* has a broad environmental tolerance to light and moisture levels, being able to recruit and grow to maturity both in open (maquis) and closed (rain forest) vegetation. A lower height growth rate among seedlings and saplings in low altitude maquis indicates that they may be more stressed and/or resource limited than plants in high altitude maquis and forest. This species provides little or no demographic evidence for a trade-off between drought and shade tolerance. The low rate of local resource depletion probably associated with the very slow growth and reproductive rates observed, and adaptations allowing tolerance of a range of light conditions, may mean that *A. ovata* largely escapes competition. Ongoing studies, which examine photosystem stress, leaf pigments and leaf and branch morphological attributes relevant to light capture and processing, will seek to identify further the extent to which this species can stretch the limits of the light/ moisture trade-off proposed by Barton (1993) and others as a major constraint on the distribution of tree species across the gradient from open to closed vegetation.

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