INVESTIGATIONS OF THE DENDROCHRONOLOGY OF THE GENUS *ATHROTAXIS* D. DON (TAXODIACEAE) IN TASMANIA

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ABSTRACT

Dendrochronological investigations in Tasmania indicate that living individuals of the two principal species in the genus *Athrotaxis,* Pencil Pine (*A. cupressoides*) and King Billy Pine (*A. selaginoides*), will provide chronologies of c. 1000 years. Older dead wood has also been collected. In Pencil Pine crossdating has been established between stands close to timberline in all the areas investigated, covering most of the range of the species, with some sites over 100 km apart. In King Billy Pine the regional climatic signal is more difficult to detect, due to low frequency growth trends and general complacency associated with the temperate montane rain forest habitat of this species. In such stands the oldest trees show the clearest crossdating. The first account of the distribution and population ecology of the two species is presented.

Les recherches dendrochronologiques effectuées en Tasmanie indiquent que des individus vivant appartenant aux deux principales espèces du genre Athrotaxis, le "Pencil Pine" (*A. cupressoides*) et le "King Billy Pine" (*A. selaginoïdes*) peuvent donner des chronologies longues de 1.000 ans environ. Du bois mort plus ancien a aussi été récolté. En ce qui concerne le "Pencil Pine" des datations croisées ont été établies entre des sites proches de la limite des arbres et provenant de toutes les régions étudiées. Celles-ci couvrent la plus grande partie de l'air occupée par l'espèce; certains sites sont distants de 100 km. Le signal climatique régional est plus difficile à mettre en évidence chez le "King Billy Pine" compte tenu de la forme des trends de croissance et de la faible variabilité annuelle d'épaisseur, associées à l'habitat de l'espèce dans la forêt tempérée ombrophile de montagne. Dans de telles situations, les arbres les plus vieux sont le plus facilement synchronisables. Le premier aperçu concernant la distribution et l'écologie de ces deux espèces est présentée.

Dendrochronologische Untersuchungen in Tasmanien deuten an, daß Bäume der beiden Hauptarten der Gattung Athrotaxis, *A. cupressoides* und *A. selaginoides,* Jahrringfolgen von etwa 1000 Jahren enthalten. Ferner wurde auch älteres, totes Holz gesammelt. Für *A. cupressoides* wurde eine Synchronisierbarkeit der Jahrringfolgen zwischen Standorten nahe der Baumgrenze nachgewiesen, und zwar für alle untersuchten Regionen, die den größten Teil des Verbeitungsgebietes dieser Art abdecken und teilweise mehr als 100 km voneinander entfernt liegen. Bei *A. selaginoides* ist der regionale Einfluß beruht auf langwelligen Wachstumstrends und geringeren jährlichen Schwankungen der Jahrringbreiten in Verbindung mit den Bedingungen der temperierten montanen Regenwaldformation dieser Baumart. Die ältesten Bäume derartiger Standorte sind am besten synchronisierbar. Es wird eine erste Darstellung der Verteilung und Ökologie beider Baumarten gegeben.

INTRODUCTION

This paper is an expansion of part of an oral presentation by the author at X INQUA Congress in Birmingham in August 1977. For a more comprehensive account of tree-ring studies of Australian trees see Ogden (1978). As far as I am aware, no descriptions of the wood structure, general ecology, physiology or phenology of the small genus *Athrotaxis* have been published, although a few remarks on these subjects have appeared in papers dealing primarily with other matters (e.g. Elliott 1951). Consequently, while the present paper is mainly a progress report of continuing research on the ecology and dendrochronology of the two principle species, it also contains the first preliminary account of their comparative ecology.

Table 1. The main distinguishing features of the two species. (*A. Laxifolia* is intermediate in all respects). Data mainly from Curtis (1975).

	A. selaginoides	*A. cupressoides*
	King Billy Pine	Pencil Pine
Tree	Usually >15 (-40)m. May form krumholz	Usually 6-15(-30)m. Rarely krumholz
Leaves	Evergreen, perennial, rhomboid ovate, loosely imbricate (tips spreading), apex acute especially in young plants.	Evergreen, perennial, rhomboid ovate, imbricate and closely appressed, apex blunt.
	6-12 mm long	2-4 mm long
Terminal branchlets	6-10 mm diameter	2-4 mm diameter
Cones	1.5 - 2.0 cm diameter c. 60 seeds/cone	1.2 - 1.5 cm diameter c. 25 seeds/cone

The genus *Athrotaxis* comprises *A. cupressoides* D. Don (Pencil Pine), *A. selaginoides* D. Don (King Billy Pine) and *A. laxifolia* Hook. The distribution and morphology of the latter 'species' strongly suggests that it is a rather infrequent hybrid between the two former, although there is no experimental evidence to support this view (Gulline 1952). It will not be considered further here. The genus is endemic to Tasmania, and the only representative of its family in the Southern Hemisphere.

The main distinguishing features differentiating the two species are annotated in Table 1. Although the species have a superficial resemblance, King Billy Pine is generally larger in all its parts than Pencil Pine.

The two species have broadly overlapping ecological requirements (Figure 1) and geographical distributions, but they are rarely found growing side by side.

Pencil Pine

Pencil Pine is of limited and discontinuous distribution in the mountains of western Tasmania and along the northern and western margins of the central plateau. Although nowhere forming an altitudinal vegetation belt, it usually occurs as small isolated stands above the *Eucalyptus* tree line. Its total altitudinal range is 620-1360 m. In some areas, e.g. the northwest corner of the central plateau, more extensive Pencil Pine forests are found, usually in the altitudinal range 1000-1300 m. Even at its upper limits Pencil Pine retains its upright conical form, and although the trees frequently have several trunks they are rarely prostrate and twisted. The highest altitude stands of small trees are frequently quite young (c. 200 yrs), but in all the areas so far investigated the largest and oldest individuals have all been found towards the upper limit of the species distribution. This distribution is clearly in part dependent upon abundant soil moisture although the species usually avoids waterlogged sites. The general regional rainfall in its areas of occurrence ranges from c. 130 to c. 290 cm/year but stands are frequently located where they probably receive localized orographic rain, moisture from cloud condensation or prolonged snow lie. As a result the species very closely coincides with the distribution of ice during the last glacial phase in Tasmania (Derbyshire et al. 1965), with many stands occurring on the rocky backwalls of the cirques. Lower altitude stands are usually associated with tarns and watercourses, and protected from fire. In such situations Pencil Pine extends into otherwise drier and colder situations than King Billy Pine. Although present (at its lower limits) at equivalent altitudes, Pencil Pine is not a component of the temperate rain forest or subalpine sclerophyll communities. Occasionally there is some slight overlap, but normally Pencil Pine stands form relatively pure monocultures. Towards its upper limits it may have *Nothofagus gunnii* (Deciduous Beech) as an understory.

King Billy Pine

Although King Billy Pine has a distribution overlapping that of Pencil Pine, in general it is a tree of the montane zone in the tall closed temperate rain-forests of western Tasmania. In such forests, King Billy trees 40 m tall may grade into krumholz forms at higher altitudes, but they are rarely found around moorland tarns further east. It occurs, therefore, in regions with an annual rainfall generally in the range 150-320 cm/year and at altitudes between c. 600 to 1270 m with best development in the wetter parts of its range between c. 750 - 1000 m. Here, large old trees, often over 2 m d.b.h., are found towards the lower limits of the species distribution, their crowns often protruding above the canopy of the associated *Nothofagus cunninghamii*, *Atherosperma moschatum* and *Phyllocladus aspleniifolius*. Pencil Pine, on the other hand, rarely grows in association with these species. In forest situations the growth form of King Billy Pine is at first narrowly conical, but the shape changes gradually with the loss of the lower limbs and expansion of the crown. Old trees usually have several large dead limbs and relatively little foliage in the crown.

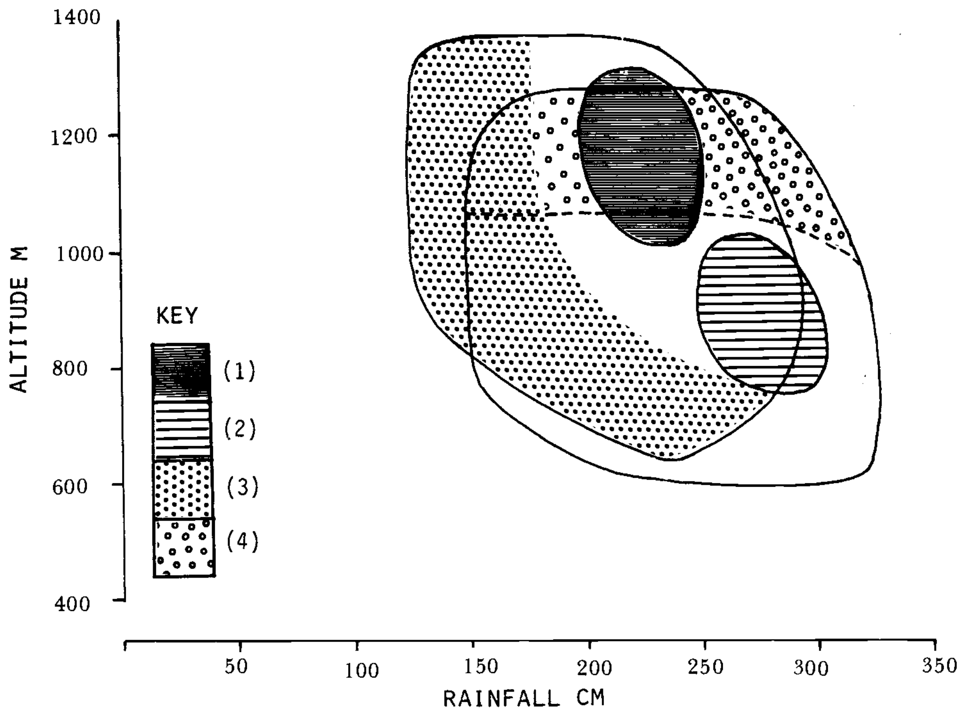

Figure 1. The ecological ranges of Pencil and King Billy Pines with respect to altitude and regional rainfall. Key: *1*, the 'optimum' for Pencil Pine; *2*, the 'optimum' for King Billy Pine; *3*, scattered individuals and small stands of Pencil Pine beside tarns and watercourses; and *4*, krumholz King Billy Pine.

RESULTS AND DISCUSSION

Phenology

The annual changes in growth rates of both species are currently being monitored in the Mount Field National Park by T. Bird of the Division of Forest Research, CSIRO. Some preliminary results are included in Figure 2. A knowledge of the phenology of these evergreen species is, of course, essential to an understanding of their climatic response functions.

Age and growth rates

Figure 3 indicates that growth rates vary in different situations, but both species may achieve ages in excess of 1000 years. At this age King Billy Pine is usually a much larger tree than Pencil Pine. Height growth particularly in the latter species can be extremely slow, especially during the prolonged seedling phase. At Mount Field seedlings 1 m tall are on average 55 years old. King Billy Pine seedlings are slightly faster growing, averaging 42 years at the same height, and there is evidence that only those individuals growing faster than average are recruited to the sapling class. In this species young trees beneath the shade of the canopy grow in height at the expense of diameter. Where it forms a krumholz it may be very slow growing, for example, trees <2 m tall with trunks c. 35 cm diameter on the summit of Mt. Read (1100m) are c. 500 years old. The average annual diameter growth rate of these trees is c. 0.4 mm/year. In contrast young trees developing in the open following a forest fire at c. 900 m on the same mountain have diameter growth rates of up to 2.0 mm /year.

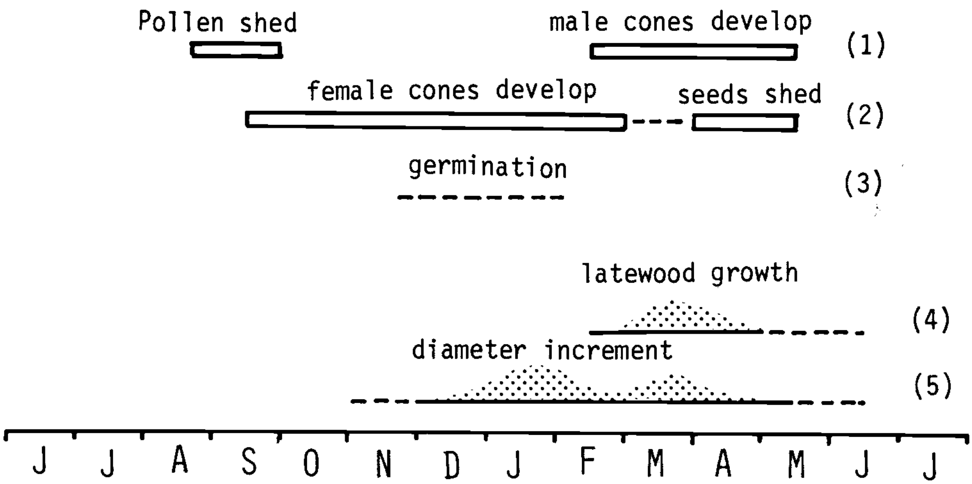

Figure 2. The phenology of Pencil and King Billy Pines. *1*, *2*, and *3*, reproductive schedule in Pencil Pine (data, in part, from Elliott, 1951); *4*, and *5*, wood growth in King Billy Pine, based mainly on data from c. 960 m on Mt Field (T. Bird, pers. comm.). Observation suggests that the reproductive behavior and wood growth of the two species is similar, although due to the higher altitude of many Pencil Pine stands its normal growing season may be shorter than that of King Billy Pine.

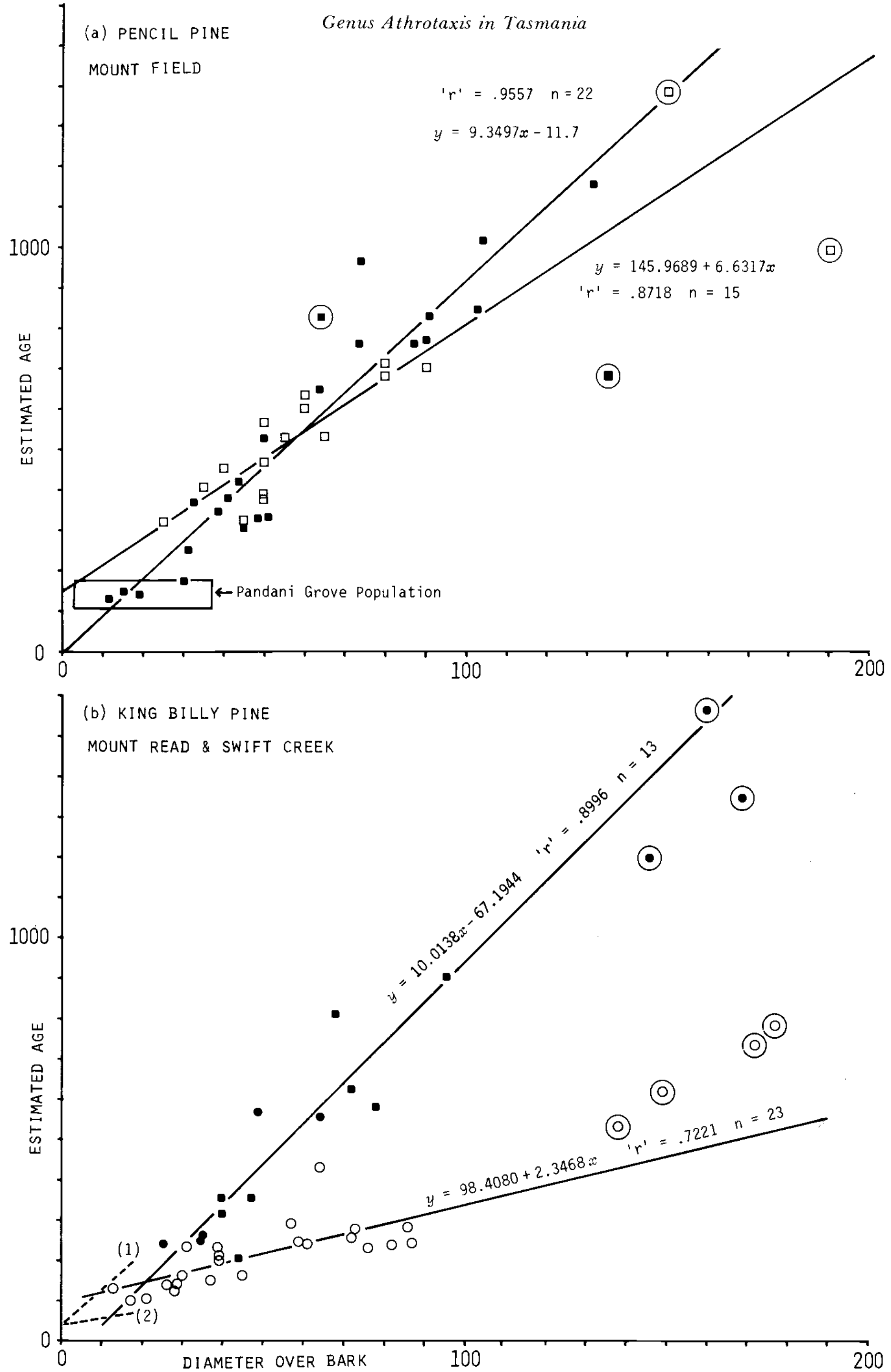

Figure 3. The age diameter relationships of (a) Pencil and (b) King Billy Pines on various sites. Key: ■ old stand of Pencil Pines on Tarn Shelf, Mount Field (site "BB", c. 1200 m); □ part of same stand c. 1 km away c. 1150 m; ● King Billy Pine stand at 750 m on Mt Read; O King Billy Pine at 880 m at Swift Creek; *1*, regression for sapling growth beneath canopy at Swift Creek; *2*, regression for sapling growth in open at Mt Read (900 m). Circled points for larger trees have a large margin of error and were not included when calculating the regressions.

Population Structure

In both species most of the stands investigated appear to consist of one, two or three generations, with quite wide gaps between them (Figure 4, *2*). In Pencil Pine 'monoculture' stands predominate and it is apparent that all individuals are approximately the same age or, if younger than average, are suppressed (Figure 4, *3*). Such stands appear to have developed in open situations which have remained 'susceptible' to recruitment of Pencil Pine for at least 100 years, but have subsequently become closed. Most of the older stands of this type date from c. 1450 but stands of earlier and later origin are known. The latter show clear evidence of density-dependent self-thinning processes. In very old stands this process, coupled with interactions with other species (e.g. *Nothofagus gunnii*) and stochastic events, leads to the isolation of individuals. The conditions stimulating the rejuvenation of very old stands, and the initiation of new ones, are beyond the scope of this paper.

Self-thining monoculture stands are also found in King Billy Pine, although often with evidence of a previous generation in the form of a few scattered older individuals. At Swift Creek, where King Billy grows associated with typical montane rain-forest species, three generations originating in the periods c. 12-1400, c. 1700 and since 1700 (mostly this century) can be recognised and related to the probable fire history of the site. On Mount Anne two generations are separated altitudinally, with the younger generation, originating mainly during the sixteenth century, being situated above the remnants of the older one (Figure 4, *1*).

The detailed histories of populations are not relevant here, but one conclusion which may have more general relevance to the dendrochronology of closed mesic forest species can be mentioned. Individuals belonging to the older generation, often with crowns protruding above the general canopy and many dead limbs, have the slowest growth rates and the clearest crossdating. At Swift Creek such trees appear to 'fit' the regional Pencil Pine chronology quite well, and certainly match similar emergent King Billy trees c. 10 km away. The subsequent generation of canopy trees (c. 270 years old at Swift Creek) are faster growing and more complacent - while they may crossdate within the site, only in exceptional years do they agree with the regional skeleton plot. Younger subcanopy and suppressed trees show no crossdating - indeed there is some indication that years which are generally unfavorable for the growth of emergent and canopy trees are favorable to these otherwise suppressed individuals, and vice versa. However this question of the interactions between different generations on a site (and interactions with other species) is complicated by the frequent radial asymmetry and partial rings of the suppressed population and must be considered still open. In general it appears that the individuals of any one generation gradually achieve better within site crossdating as the stand ages and mortality removes the suppressed fraction. Sensitivity to the regional climatic pattern is not fully achieved until this process, and perhaps subsequent senescent die-back, has isolated individuals within the forest. This generally takes over 300 years in the case of King Billy Pine. This knowledge has clear implications for dendrochronological sampling strategy in rain-forest stands of this species.

Dendrochronological Investigations of Pencil Pine

The numbers of sites being studied and their sample sizes are given in Table 2. In addition some material has been collected by other workers. The distribution of the main sites is shown in Figure 5. Skeleton plots have been completed for most of the major Pencil Pine sites in one case (Mt. Field) covering the period 1027 to 1976. The full chronologies are not yet completed, and for the present purpose of illustrating the potential of the species only the period 1885-1915 is shown in Figure 6. This restricted period is one in which several characteristic narrow rings occur, allowing easy comparison between sites and species. Missing rings are rare in Pencil Pine and the presence, on any one site, of synchronous 'frost rings' gives confidence in the crossdating. The frequency of frost damaged rings is being analysed, but in most cased they appear to be of local rather than regional significance, and mainly affect younger trees which were growing in relatively open situations.

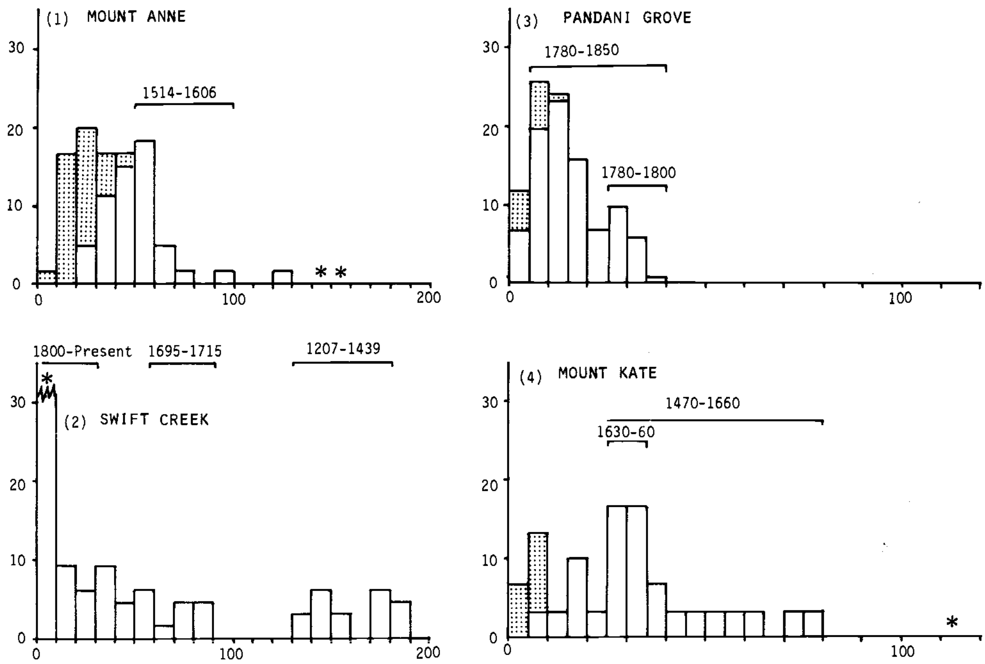

Figure 4. Examples of size-class frequency distributions in some of the sites from which chronologies are being developed. *1*, and *2*, King Billy Pine; *3*, and *4*, Pencil Pine. Key: shaded areas represent dead or dying individuals (not recorded in *2*). *indicates (more) trees present in this class but not included in the frequency distribution sample. The periods during which particular size classes became established are indicated by horizontal bars. *1*, and *3* are examples of self-thinning stands in which subsequent regeneration has been suppressed. *2*, and *4* are examples of more complex populations with more than one generation present. Class intervals are 0 to <10 cm d.b.h. etc. for King Billy, and 0 to <5 cm d.b.h. etc. for Pencil Pine.

Table 2. Pencil Pine sites in Tasmania.

Geographical location	Number of sites		Sample Size			Skeleton plot completed
	Major > 20 trees	Minor < 20 trees	Individuals	Cores	Segments	
Pine Lake	1	1	46	54	9	1480-1976
Swifts Creek area	0	1	14	14	4	n.a.
Mount Kate/Waldheim	0	4	32	42	0	1480-1976
Mount Field	8	4	240	245	203	1027-1976
Dickson's Kingdom	0	4	51	63	4	1518-1976
Totals	9	14	383	418	220	

n.a. – not fully analysed.

Figure 6 demonstrates very good crossdating between small samples from sites covering almost the total range of Pencil Pine. Pine Lake, Mount Field and Mt Kate are respectively the most eastern, southern and northern sizable stands of the species, although a few very small stands are found beyond these limits. At Mount Field a large number of sites have been studied and a chronology of about 1000 years has been established. Older material may be hard to find, although there are reports of buried logs in a few localities. Most of the apparently old sites appear to date from the 14th or 15th century. Figure 6 also illustrates that sites only short distances apart may show rather different behavior - for example the 1904 ring at Mt Kate 3. This is due to local events, severe snow falls, storms, fires etc. which can be very valuable in understanding the population behavior.

At Mt Field several crossdating sites at different altitudes are being studied. As yet only one of these, Pandani Grove, has been fully analysed (Figure 7). The age distribution of this stand is illustrated in Figure 3 and a size frequency distribution in Figure 4, 3. The stand is situated at a relatively low altitude (1040 m) on a damp level area in a valley between two tarns. It is relatively young and complacent, and clearly undergoing self-thinning at present. Frost-ring analysis indicates that the area was more open when the young trees were becoming established. The chronology from this site extends back only to 1810 and accounts for only 20 percent of the variance of the tree rings, but this is to be expected from the nature of the population and the sites it occupies. Other sites on the mountain are known to be more sensitive and to have much longer records.

Dendrochronological Investigations of King Billy Pine

Details of the sites are given in Table 3 and Figure 5. Although old living individuals of King Billy Pine and dead wood well over 1000 years old are known, progress with chronology building has been slow due to the sample selection problems already discussed, and because the ring characteristics of this species render it more difficult to crossdate than Pencil Pine. There is considerable radial variation in growth rates, with the fastest growing radii changing from time to time, perhaps in response to branch development, shading and abscission in the crown. Single rings, or groups of up to 20 rings, may be totally absent on some radii. This presents problems for the dendrochronologist: initial examination must be based on trunk segments, not cores,

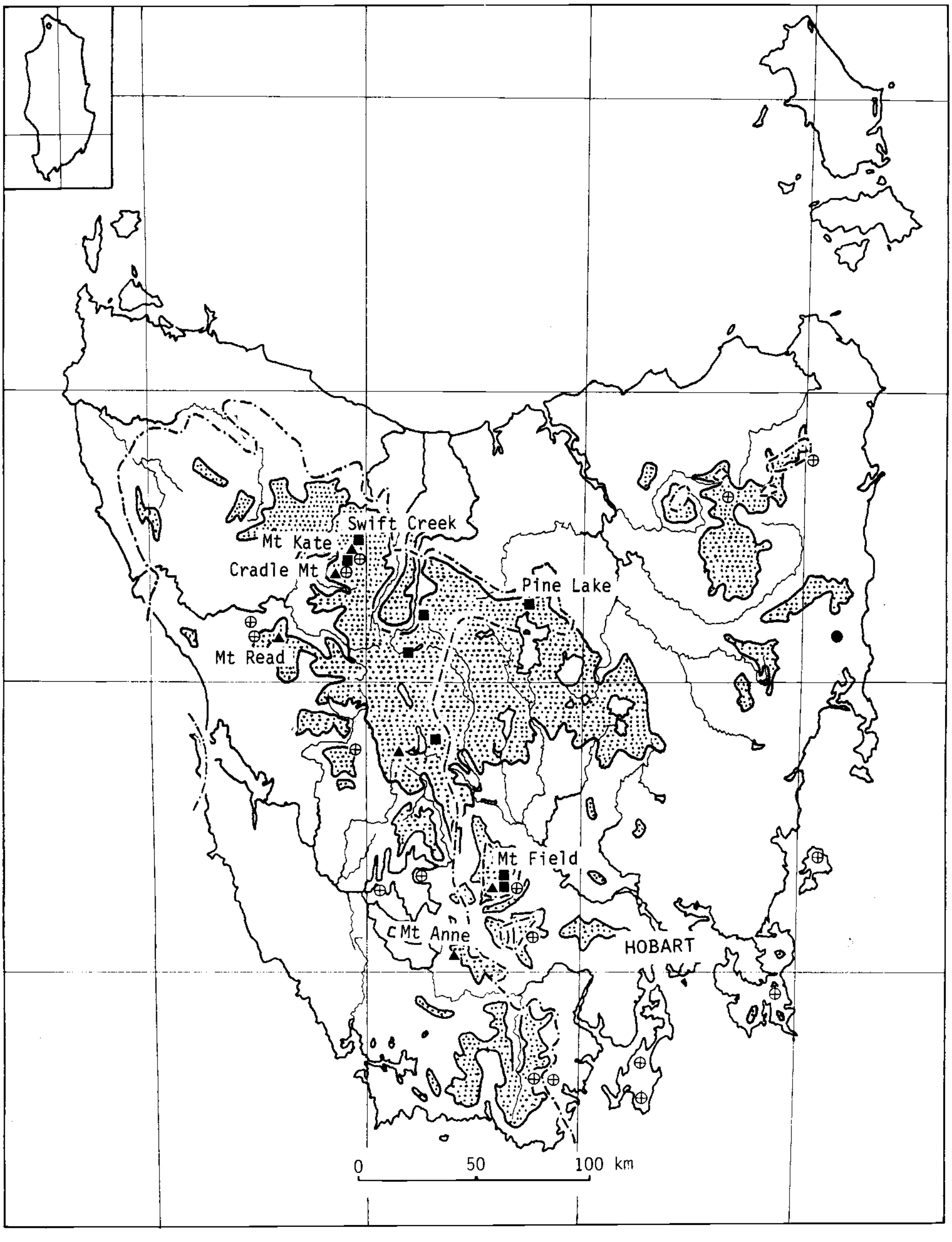

Figure 5. Map of Tasmania showing the main dendrochronological sites under investigation by various workers at present. Key: ■ Pencil Pine sites; ▲ King Billy Pine sites; ⊕ *Phyllocladus* sites; ● *Callitris* sites. Land above c. 610 m is stippled. The broken (dot-dash) line shows the approximate position of the 150 cm isohyet.

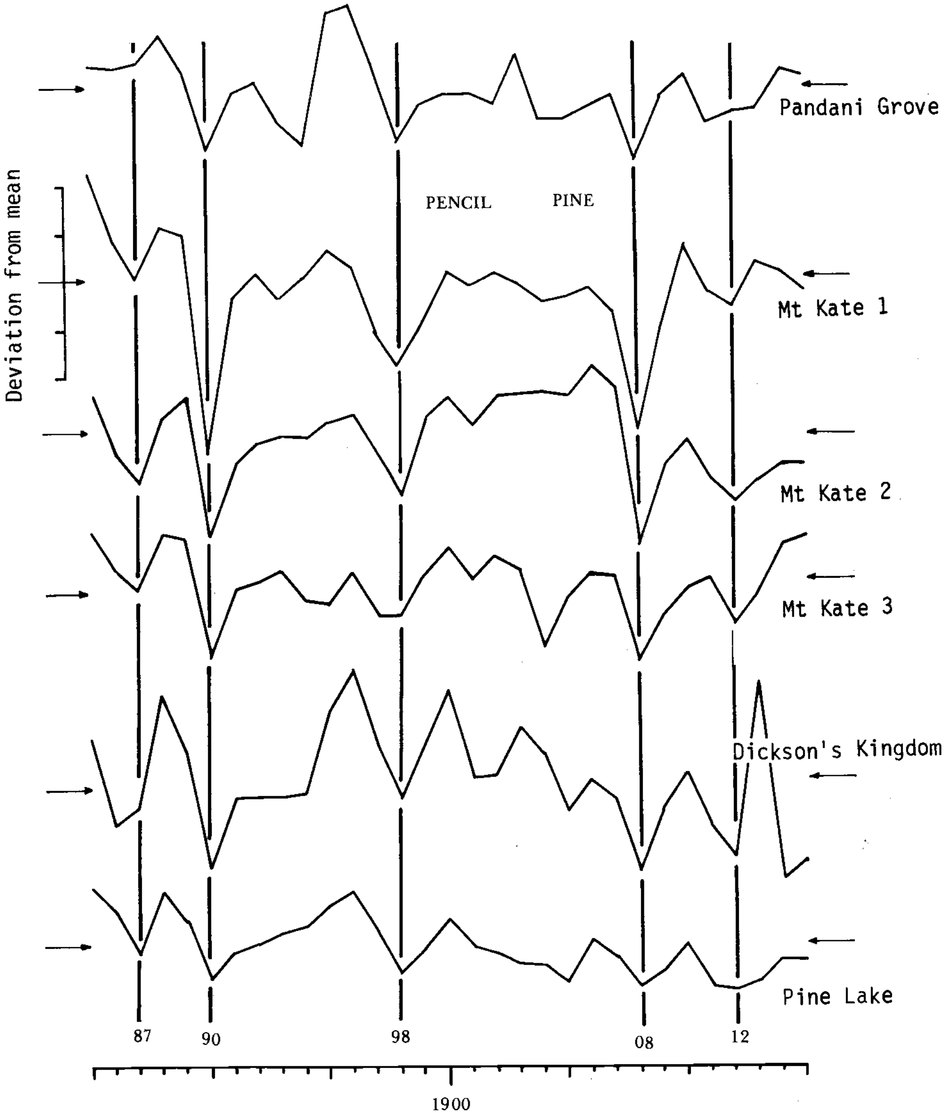

Figure 6. Crossdating between widely separated sites of Pencil Pine. The curves were obtained by subtracting the individual ring width from the mean, indicated by the horizontal arrows, and are based on a subsample of three representative trees from each site. Three subsites at Mt Kate, situated at different altitudes are shown. The vertical lines indicate the characteristic narrow ring signature for this period.

and even if crossdating can be achieved series of raw ring-width measurements normally contain low frequency growth trends which are not common between trees (or between radii) and are presumably nonclimatic in origin. In addition, because the species generally grows in rain-forest in a relatively mild humid climate it is not very sensitive to annual variations in rainfall and temperature. When in the sapling and pole stage marked ring-width variability is mainly due to local competitive influences -the opening or closure of the canopy. Once the canopy has been reached the rings show relatively little variation from year to year until senescence. The large old trees are invariably growing in rain-forest situations, where they may not be subjected to climatic extremes so frequently as Pencil Pines at timber-line and where much of the growth ring variability must arise from local biotic (competition) effects. Figure 8 illustrates the fact that careful choice of material may give very close agreement between sites, but due to a predominance of non-climatic variance, "noise", lumping together all certainly dated individuals on a site may produce a rather insensitive chronology. Old senescent trees, over 1 m d.b.h., are slow growing and relatively sensitive, and these are being used to build a detailed chronology for the Swift Creek site. The species has dendrochronological potential due to the considerable age reached by living trees, and because the dead wood is very resistant to decay. For example, at Waldorfer's forest (c. 8 km from Swift Creek) living trees c. 1000 years old are known, segments from logging operations with 900 rings have been collected, and sound fallen logs of the forest floor have had their centres radiocarbon dated at between 1275±150 and 1715±140 B.P. (GX 4896; GX 4898).

Progress is being made in Tasmania with climatic reconstruction using carbon isotopes (Pearman et al. 1976). Pearman and his colleagues at the CSIRO in Melbourne have established a tentative relationship between temperature and the ratio of carbon isotopes in King Billy Pine wood, which if verified, could serve as a basis for palaeotemperature reconstruction. So far this is the only species analysed, and at only one site (Swift Creek), but the work is being expanded at this and adjacent sites on a number of species.

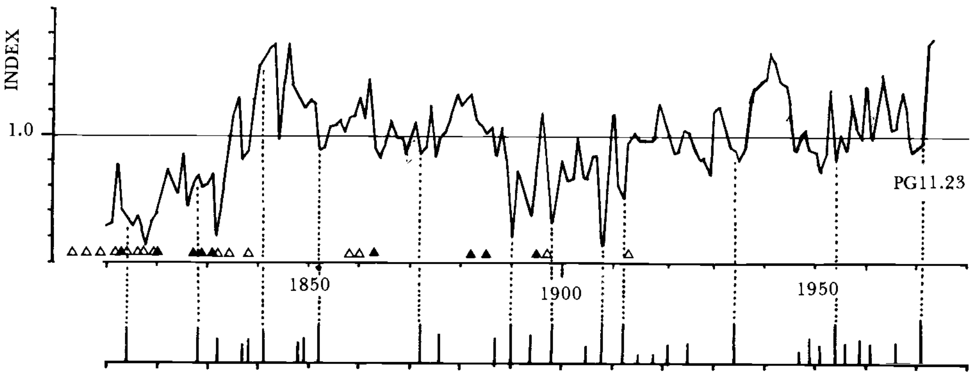

Figure 7. Pencil Pine chronology, Pandani Grove. Based on 23 radii from 11 trees. The lower part of the figure is the regional Pencil Pine skeleton plot. Note that Pandani Grove agrees well with it after c. 1850, but before then when the trees were growing rapidly and the site was open, the match is poor. Open triangles indicate frost rings on individual trees, closed triangles frost rings that crossdate between individuals on the site.

Table 3. King Billy Pine sites in Tasmania.

Geographical location	Number of sites		Sample Size			Skeleton plots completed
	Major >20 trees	Minor <20 trees	Individuals	Cores	Segments	
Mount Read	1	2	45	22	38	n.a.
Swift Creek	1	0	48	15	47	1560-1976
Mount Kate/Waldheim	1	2	65	45	37	n.a. pre 1550
Mount Field	1	4	54	57	0	n.a.
Mount Anne	1	0	22	34	0	1425-1976
Totals	5	8	234	173	122	

n.a. = not fully analysed

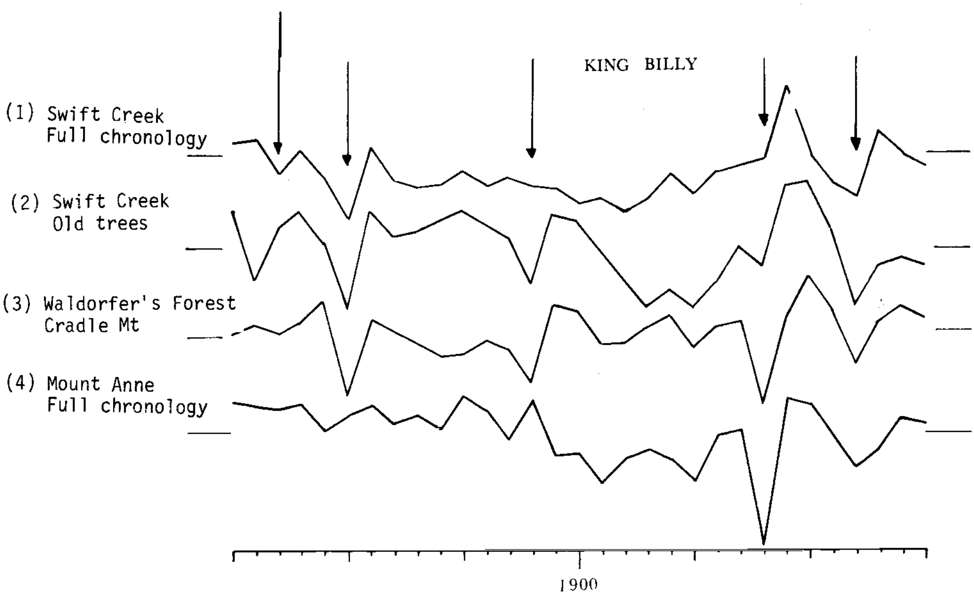

Figure 8. Crossdating between widely separated sites of King Billy Pine. The vertical arrows indicate the Pencil Pine signature rings for the same period. The curves are based on the following sample sizes (trees: radii); *1*, 20:42; *2*, 4:6; *3*, 3:5; *4*, 15:19.

CONCLUSIONS

In order to put the current work on *Athrotaxis* into proper perspective I should, in conclusion, mention that work is also progressing on the dendrochronoloty of a number of other endemic Tasmanian conifers, notably *Phyllocladus aspleniifolius.* Much of this work is being carried out by V.C. LaMarche of the Laboratory of Tree-Ring Research in Tucson. Because the chronologies developed from various sites for *Phyllocladus* are to a degree correlated with those of Pencil Pine, the preliminary response function analysis of this species (V.C. LaMarche, pers. comm.) sheds some oblique light on the response of Pencil Pine. It appears that severe drought years are sometines recorded in the year in question, but perhaps more frequently (in Pencil Pine), in the subsequent years. However, with a timberline species such as Pencil Pine it seems probable that summer temperatures will also influence growth - indeed it is rather surprising to find even severe drought years, such as 1908, so clearly recorded by this species. Although at the moment I can draw no conclusions about climatic responses or climatic calibration, I can stress that the various different species under investigation have different - but not completely different - chronologies, implying that they have different response functions and giving promise of a detailed climatic reconstruction for Tasmanian covering the last 1000 years.

ACKNOWLEDGEMENTS

Thanks are due to Professor V.C. LaMarche with whom I have cooperated at various stages in the work. I should also like to thank those who have helped me in the field, in particular Mr. T. Bird of the CSIRO Division of Forest Research, and Dr. C. Harwood. Research work on the species would not have been possible without the permission of the National Parks and Wildlife Service of Tasmania, and the cooperation of several park rangers.

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