

FACTORS INVOLVED IN THE RECENT MORTALITY OF PLANTS FROM FOREST AND SCRUB ALONG THE LAKE TE ANAU SHORELINE, FIORDLAND

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SUMMARY: Mortality of forest and scrub species from most deltas of the Lake Te Anau shoreline is described following unnaturally prolonged flooding during 1975. Despite a high incidence of pinhole borer in the affected beech trees there is conclusive evidence that the mortality in most species was due to prolonged high water tables that exceeded the tolerances of many important shoreline species. Differential mortality in *Leptospermum scoparium* (manuka) apparently depended on whether or not plants were totally submerged for substantial periods—their root systems appear to be tolerant of indefinite flooding.

The results have substantiated previous predictions on submergence tolerance of species from lake-shore forest and scrub communities. These tolerance values had been derived by indirect methods and form the basis of the high-level operational guidelines for use of the lake waters for hydro-electric generation.

INTRODUCTION

Recent studies of shoreline vegetation of Lakes Manapouri and Te Anau (Johnson, 1972a, 1972b; Mark *et al.*, 1972) were aimed at assessing the tolerances to submergence and emergence of species from the various zones. These assessments were based on the elevational limits of each species in relation to the patterns of natural lake level variation recorded daily for each lake over a 37 year period. Although indirectly assessed, these tolerance values were used in 1973 by the Guardians of Lakes Manapouri and Te Anau as the basis for establishing guidelines, particularly in the high operation range, for the use of each lake for hydro-electric generation (Mark and Johnson, 1972).

During 1975 these guidelines were exceeded when high lake levels occurred for unnaturally prolonged periods at both Lakes Manapouri and Te Anau but particularly at Lake Te Anau where the control structure, recently commissioned at its outlet, was operated to reduce outflows in an attempt to protect the incomplete and vulnerable dam construction works at Mararoa, downstream from Lake Manapouri. The guidelines were exceeded on two separate occasions, April-June and August-December, at Lake Te Anau but only one of these at Lake Manapouri. The duration of the excess depends on difference in interpretation (Figs. 1 and 2).

Mortality of shoreline plants was first observed in October 1975 when a few dead small-trees of kahikatea (*Dacrycarpus dacrydiodes* (Rich.) de Laubenfels*) was seen at two sites on Lake Manapouri (Holmwood Island and between Calm Bay

and Buncrana Island) and at Mussel Cove, Lake Te Anau. The large deltas on Lake Te Anau were not visited until late December when many recently dead and dying trees, mostly beech, were noticed.

During February 1976 four days were spent in examining the 20 largest deltas on the Lake Te Anau shoreline. On 16 of these, recently killed woody plants were present—only the deltas of the Eglinton River†, Tutu Burn, Nurse Creek, and Safe Cove appeared to show no mortality. Occasional dead trees were present on sandy beaches not associated with deltas as on the north side of the Worsley Arm near its head but no abnormal mortality was seen along rocky sections of the shoreline nor on any of the extensive sandy beaches such as at Brod Bay and Dock Bay.

METHODS

Seventeen sites on 11 deltas were selected for study and at each, observations were made on the distribution of dead plants, their species, elevation relative to the lake, and size. In the case of the beeches, both silver and mountain (*Nothofagus menziesii* and *N. solandri* var. *cliffortioides*), living trees of the same species and similar size closest to each dead one were similarly examined and incre-

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* Nomenclature follows Allan (1961) and Moore and Edgar (1970) except where authorities are cited.

† Most place names referred to in this paper are shown in Figure 1 (p. 144) of Mark *et al.*, (1972).

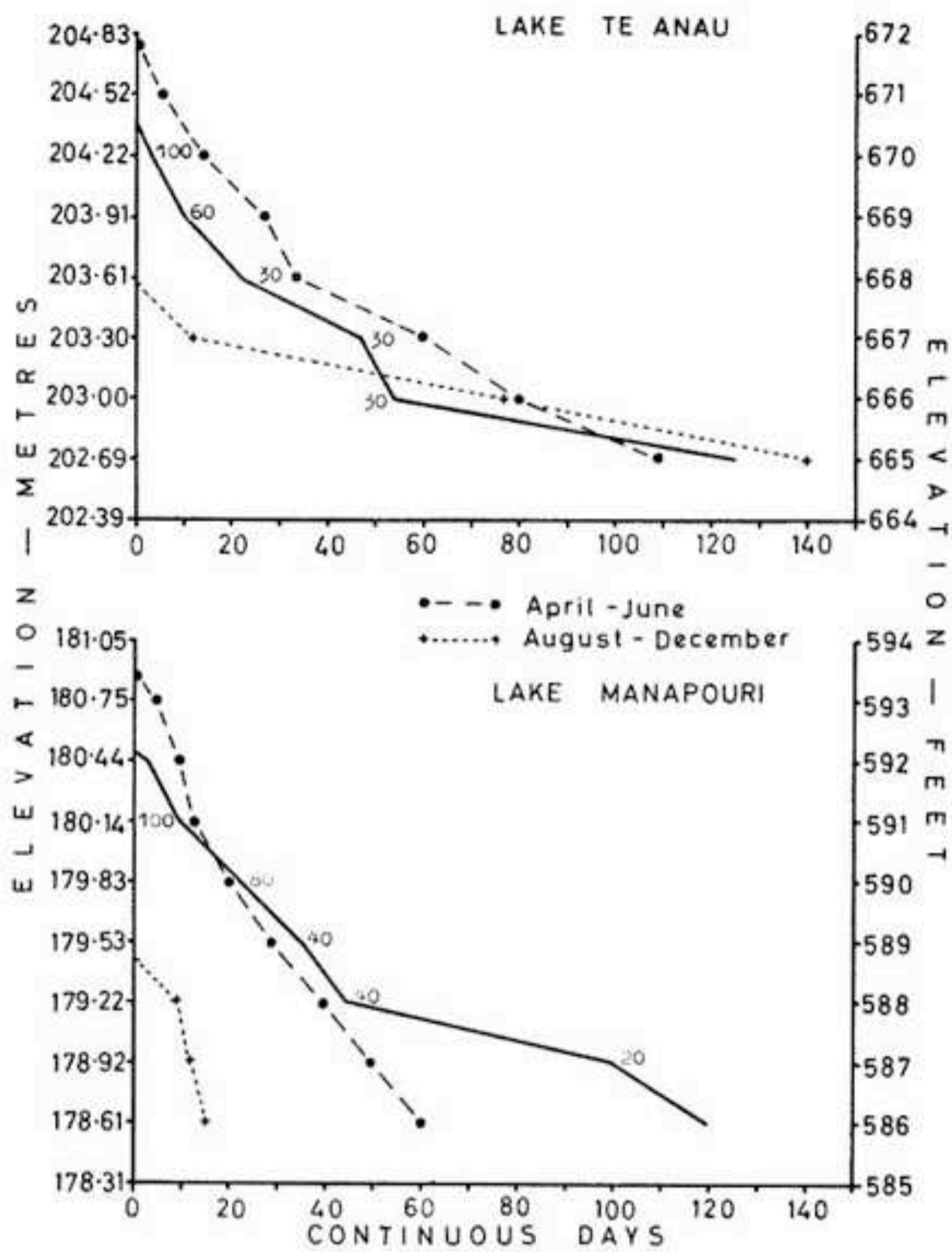


FIGURE 1. Guardians' guidelines for the high operating ranges of Lakes Te Anau and Manapouri (solid lines) based on a previous study of flooding tolerances of lakeshore vegetation (Johnson, 1972b), compared with lake regimes for two periods in 1975. Numbers adjacent to the guideline curves are specified minimum intervals (days) to be exercised between consecutive floods reaching that particular level (to provide for adequate drainage of water tables). Lake regime values for 1975 are based on the actual duration, in continuous days, regardless of whether the specified minimum intervals were achieved (cf. Fig. 2).

ment cores taken from a sample of these paired trees in order to compare diameter growth patterns of the two groups, particularly in relation to lake level variation and drought and flood years. Thus no pair was erected unless there was mortality. When it was noticed that dead beech trees tended to have infestations of pinhole borer (*Platypus* spp.) its incidence on both dead and live tree pairs was also recorded. Soil pits were dug at 11 sites, usually adjacent to dead trees. More detailed observations on the role of pinhole borer were made during two days in

June with Mr R. H. Milligan, forest entomologist, N.Z. Forest Service. At this time it was obvious that mortality among beech trees had continued, particularly involving trees that had shown partial death in February. In order to assess this trend all dead and obviously dying beech trees plus a few of wineberry (*Aristotelia serrata*), 66 trees in all, in the vicinity of the hut and on the northern side at the head of the Worsley Arm of the lake, were tagged by Park Board staff in July and reassessed 10 months later (May 1977). Since no further mortality has been observed at Lake Manapouri no studies were initiated there.

For the analysis of the data on the beech trees, the fate of each tree was scored as zero for a dead tree and one for a live one. Regression analysis could then be used to examine the relation between several

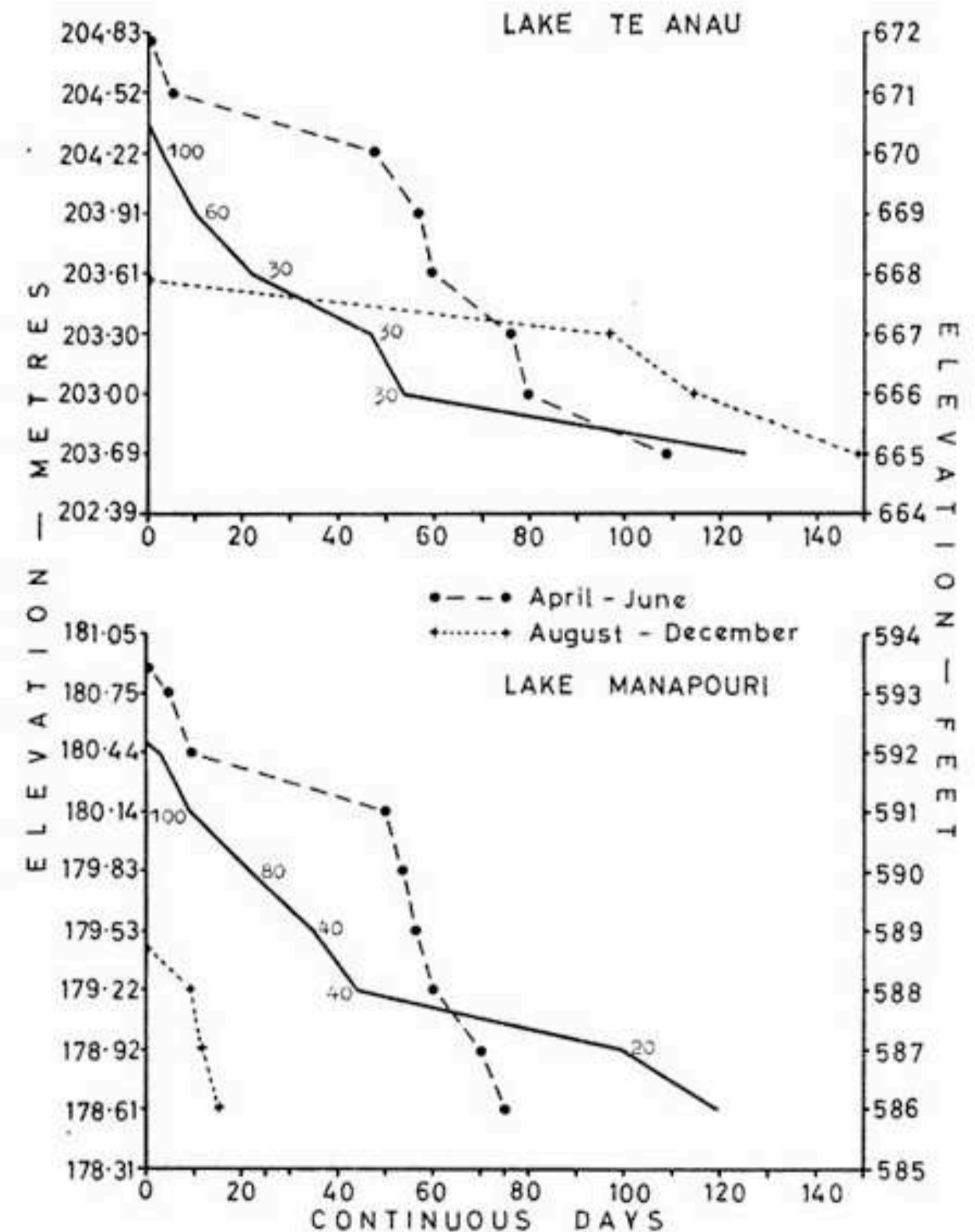


FIGURE 2. Guideline values as for Figure 1 for Lakes Te Anau and Manapouri. Lake regime values for the two periods in 1975, as distinct from Figure 1, have also included days when each lake dropped below the particular level, in those instances when the "specified minimum intervals between consecutive floods" were not achieved.

factors and the death of trees. The factors it was possible to include were: (a) elevation, (b) presence or absence of pinhole borer (cases where this had not been established in the early part of the study were treated as a third class of infestation), (c) species of beech, (d) interactions between these three factors, (e) the site and (f) which pair within the site the tree was a member of.

A multiple regression was therefore used, in which all or some of the above factors were taken as the independent variates, predictors of the dependent variate, life/death. The advantage of this approach is that whilst there may be correlation between the predictor factors, a multiple regression shows the relations between these factors and life/death, adjusted for any such correlations. The whole regression shows to what extent the death of the trees can be accounted for in terms of these factors. Because of the correlations between the predictor factors, their individual effects cannot be calculated directly, but they can be estimated in two ways: i. from the sign and magnitude of the regression coefficient; ii. from the decrease in the efficiency of prediction of life/death when any single factor is removed from the regression. Variation unaccounted for would include environmental factors not measured, limit-

ation of recording tree condition as only a two-state (live/dead) variate without intermediates, and chance.

RESULTS

Extent of Mortality and Species Involved

Dead beech, both silver and mountain, were the most numerous and conspicuous of the recently killed plants, ranging in size from small-trees to over-mature trees of 140 cm d.b.h. and 30 m high. Dead seedlings and saplings of beech, however, were extremely rare. Only a few of the dead trees appeared to have been competitively disadvantaged. Indeed most were mature stems of good form and many, either along the outer forest margin or as outliers among scrub, appeared to have been vigorous specimens. Dead plants were almost confined to the large deltas viz. Clinton River (mostly c. 1 km above the mouth opposite Glade House), Worsley River, Glaisnock River, Narrows, Lugar Burn, Wapiti River, Doon River, Junction Burn, Snag Burn, Ettrick Burn, Esk Burn, and Delta Burn, with only an occasional dead tree at Sandfly Point, Billy Burn, Chester Burn and Gorge Burn.

The number of beech stems and other species actually documented are listed in Table 1, together

TABLE 1. Details of elevations and plant sizes of recently killed and some adjacent surviving plants of 12 species from the Te Anau lake shore. February 1976.

Species	No. of specimens	Elevation (m)		Height (m)		Diameter (cm)	
		mean	range	mean	range	mean	range
LIVE							
<i>Nothofagus menziesii</i>	38	203.59	203.00–204.23	17.5	5–30	47.5	4.8–140.0
<i>N. solandri</i>							
var. <i>cliffortioides</i>	29	203.62	203.19–204.12	18.4	12–26	37.5	14.0–92.4
<i>Weinmannia racemosa</i>	7	203.73	203.39–204.72	10.4	5–17	13.1	5.6–23.8
DEAD							
<i>Nothofagus menziesii</i>	51	203.50	203.08–203.82	16.4	9–30	43.0	9.3–140.0
<i>N. solandri</i>							
var. <i>cliffortioides</i>	34	203.49	202.76–204.04	17.6	9–30	38.2	12.9–85.4
<i>Weinmannia racemosa</i>	13	203.55	203.30–203.81	10.4	6–22	18.6	9.1–36.0
<i>Pseudowintera colorata</i>	17	203.31	202.70–203.78		1–2.3		
<i>Blechnum minus</i>	5		202.70–203.78				
<i>Dacrycarpus dacrydioides</i>	3		202.60–203.10		9–30		15.3–129.6
<i>Leptospermum scoparium</i>	4		202.22–202.34		0.5–2.7		
<i>Dacrydium cupressinum</i>	1		202.56		13		25.4
<i>Coprosma propinqua</i>	3		202.22–202.34		1–2		
<i>Rubus cissoides</i>	2		203.14–203.35		8		
<i>Phyllocladus alpinus</i>	1		203.75		1.5		2.3
<i>Carmichaelia sp.</i>	1		202.67		0.4		

with values for elevation, plant height and diameter where appropriate. In addition to those tabulated, dead plants of *Carpodetus serratus*, *Griselinia littoralis*, *Coriaria arborea*, *Dracophyllum longifolium* and *Cyathodes juniperina* were also observed. All were located either close to the lake edge or surrounding depressions created by storm beaches along the lake shore, e.g. Snag Burn; Lugar Burn. The dead plants were at or near the lower limits of the respective vertical ranges of their species (Fig. 3) and in the case of the beeches, dead trees were significantly lower in elevation than their nearest living neighbour. Although the fitting of the statistical model reduced the sum of squares by a non-significant amount (from 28.5 with 113 degrees of freedom to 10.6 with 46 d.f.) the estimates of effects of the predictors in the model established only the effect of elevation as significant ($p < 0.05$).

No dead plants were recorded of *Elaeocarpus hookerianus*, *Pittosporum colensoi*, *Pseudopanax simplex*, *P. colensoi*, *Myrsine divaricata*, *Coprosma parviflora*, *Neomyrtus pedunculata* or *Blechnum discolor*, even within the elevation range of mortality in other species.

Symptoms of Death

The crowns of all affected beech trees were conspicuous in December and February by the brown colour of their dead foliage, all of which remained attached even though most trees were completely dead. Some trees had a few living branches and on

trees with epicormic shoots these were often still alive on the lower 5-8 m of trunk in February. Kamahi (*Weinmannia racemosa*) trees were either wholly alive or entirely dead, retaining a full complement of dead brown leaves. Indeed, only peppertree (*Pseudowintera colorata*) failed to retain all its dead leaves.

Some manuka (*Leptospermum scoparium*) stems, mostly smaller ones along the outer edge of the shrub zone, were completely dead but in most, only the lower foliage had been killed although it was still attached, while the upper foliage appeared quite normal—on the Snag Burn delta the critical elevation separating dead from living foliage was measured at 203.04 m a.s.l. The lowermost plants of *Blechnum minus* were consistently dead. Most of the dead beech foliage was still retained in June except that trees that had died between February and June were obviously shedding leaves in June.

Foliage death of a different type was noted in February on other beech trees of both species in the vicinity. Here leaves on lower branches were partially or completely brown while those on higher branches were more healthy and the crowns appeared normal. Close examination of trees with these symptoms indicated that foliage death was associated with heavy flowering. The dead parts comprised leafy twigs 5-10 cm long containing spent male flowers, that appeared to predominate on the lower branches. Maturing nuts were abundant on branches with healthy foliage in the upper crowns of these trees. Trees, particularly of mountain beech, with these features were seen at several shoreline sites, but they were also common at higher elevations and none appeared to succumb. The same phenomenon was reported from the Manapouri-Te Anau area in late January by the N.Z. Forest Service (Mr J. D. Slater-Hayes, pers. comm.).

Pinhole Borer Incidence

In February most of the dead beech trees, but few of the living ones, contained pinhole borer, detected by the characteristic fibrous dust of adult frass on their trunks (Table 2). Many of the dead kamahi stems were also affected. No larval frass was observed in February or June, indicating that infestation had been quite recent. In June Mr Milligan established that all three species of *Platypus* (*P. apicalis* White, *P. caviceps* Broun and *P. gracilis* Broun) were present. Adult frass was more abundant and conspicuous on trunks of the dead trees than it had been in February and by now almost all but the stems were heavily infested. By contrast, very few of the living trees that were being attacked in February showed any activity in June though they had inactive pinhole burrows with typical pathological wood and

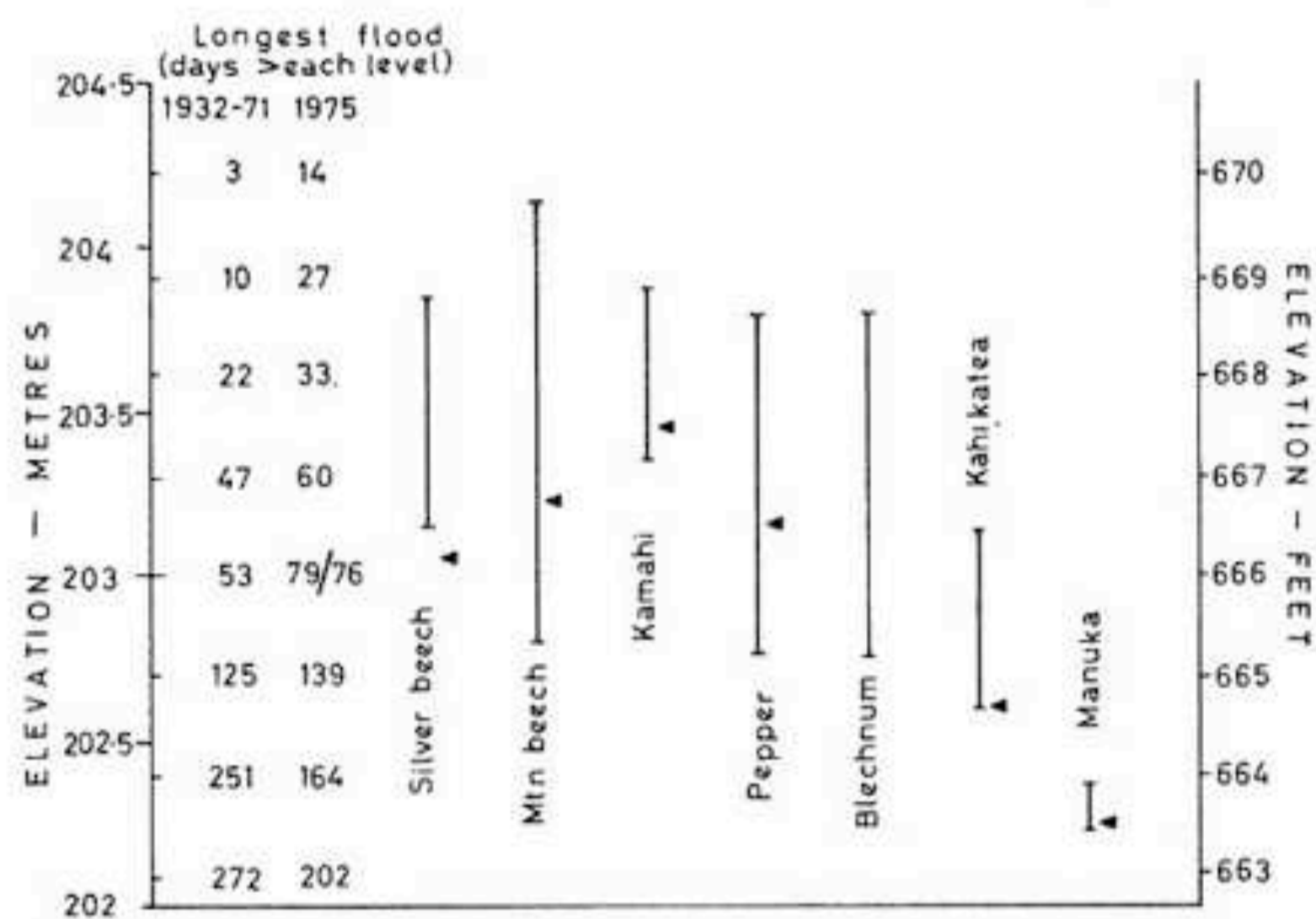


FIGURE 3. Ranges of elevations for dead plants of seven species along the Te Anau lake shore. Values are also given for the longest floods (continuous days) in the 40 year period of natural conditions (1932-71) and those for 1975. The small arrows indicate the lowest elevations of surviving plants for six of the species.

TABLE 2. *Pinhole borer incidence in beech trees along the Lake Te Anau shoreline. February 1976.*

		borer	no borer
Silver beech	dead	30	8
	live	3	25
Mountain beech	dead	20	3
	live	10	19
		63	55

gum barriers produced by the outer living sapwood (Milligan, 1972). Light infestations of pit-weevil (*Psepholax* sp.) and the beech buprestid (*Nascioides enysi* Sharp) were noted among the dead trees at this time. In addition the white vegetative hyphae of *Armillaria* root rot fungus had reached a height of 1.4 m beneath the bark on many dead stems.

Soil Profiles and Water Tables

Eleven soil pits, usually adjacent to some dead beech trees either near the forest edge or in depressions behind storm beaches, showed generally fine textured material at most sites. In eight of the pits the water table was 4-29 cm (mean 11.4 cm) above lake level; only in one was it below, by 3 cm. No water table was evident in two of the pits, one of which was excavated to 5 cm below lake level.

Beech Diameter Growth in Relation to Mortality, Pinhole Borer Attack and Seasonal Lake Levels

Ring widths for the last 25 years in 50 pairs of adjacent live and dead beech trees (28 pairs of silver beech) from 15 of the 17 sites studied were examined. A linear regression model was calculated similar in method to that used for the live/dead data, relating ring widths to: a) elevation; b) presence or absence of pinhole borer; c) species of beech; d) whether the tree was alive or dead. This revealed no significant difference with species, mortality, or elevation but trees with pinhole borer attacks had significantly greater ring widths ($p < 0.01$).

In examining the year-to-year variations there was a problem in that ring widths were not available from some of the trees for some of the early years. In order to avoid loss of information from these trees and also to avoid any bias due to the exclusion of certain trees from the mean for some of the early years, the residuals (unexplained variation in ring width) for any year were meaned and added to the overall mean to give a value for the mean ring width in that year, adjusted for any bias through the exclusion of some trees.

Relating these adjusted means to seasonal variation in lake level (extreme maximum and mean maximum; extreme minimum and mean minimum) for the current "summer" (September-February) and previous "winter" (March-August) (Fig. 4), revealed an effect of all four measures of lake levels. The marginally best fit for each season was with extreme maximum and mean minimum respectively. With winter extreme maxima the results indicate that the highest levels (> 204.5 m) depressed the following season's ring width by about 3.3 mm whereas the lowest values caused only a slight reduction, c. 0.4 mm (Fig. 4). With summer mean minima on the other hand, results indicate that both high and low values (202.45 m and 201.38 m respectively) reduced the width of that season's growth ring by an equal but intermediate amount, c. 1.3 mm (Fig. 4).

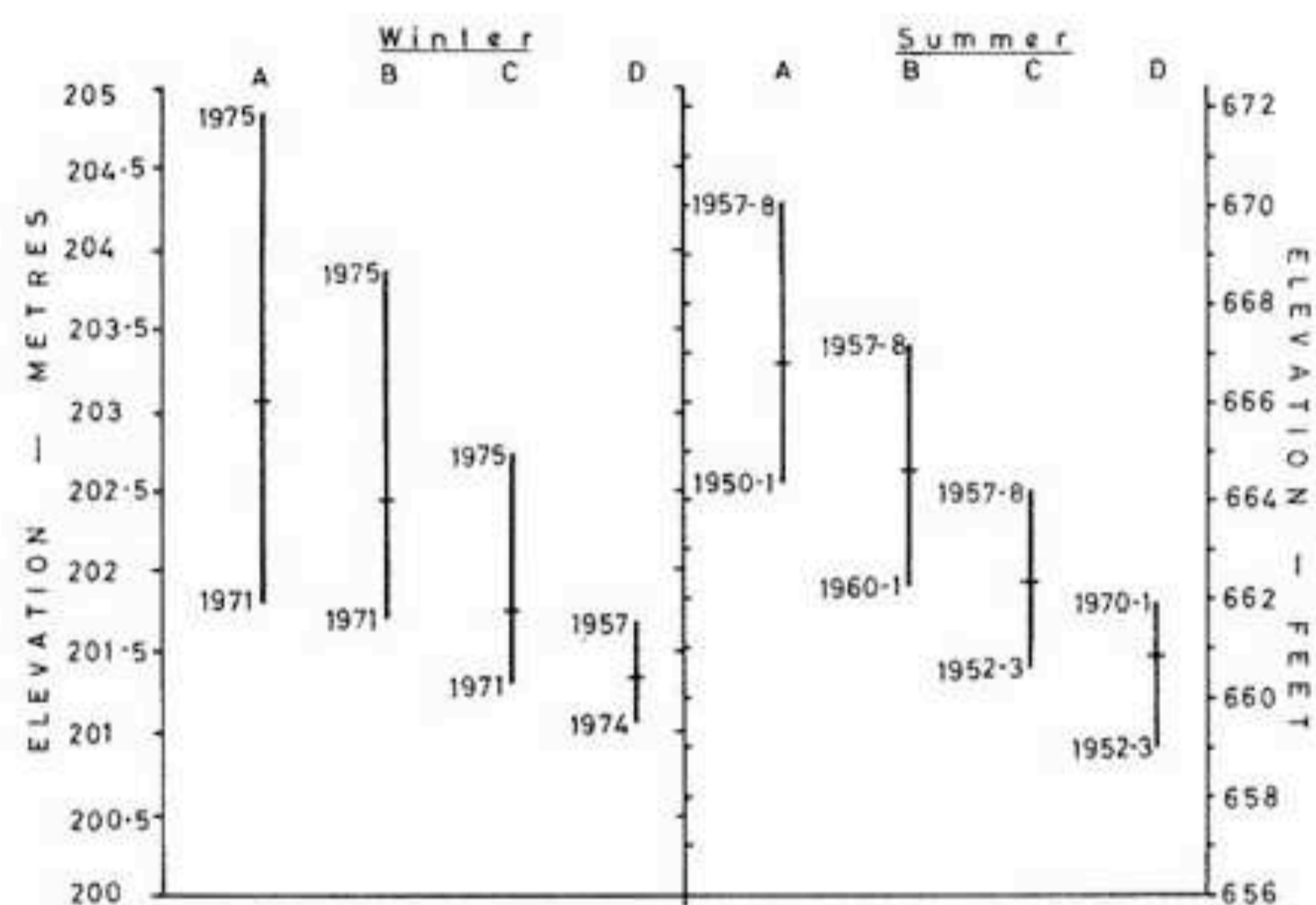


FIGURE 4. Annual range of lake level values recorded for Lake Te Anau for a 26-year period (1950-76). Values are given separately for "winter" (March-August) and "summer" (September-February) and have been partitioned to show values for extreme maxima (column A), mean maxima (B), mean minima (C), and extreme minima (D) for each 6-monthly period. The years representing the extreme variants are shown.

Indications from the curve fitted to ring widths and low lake levels in summer support the previous findings of significantly reduced ring width produced during the droughty 1970-71 season (Mark *et al.*, 1972). Moreover, the considerable variation apparently unrelated to these lake level parameters revealed in the present analysis, might explain the failure in the earlier study to demonstrate significantly reduced diameter growth during a single particularly wet season (1957-58).

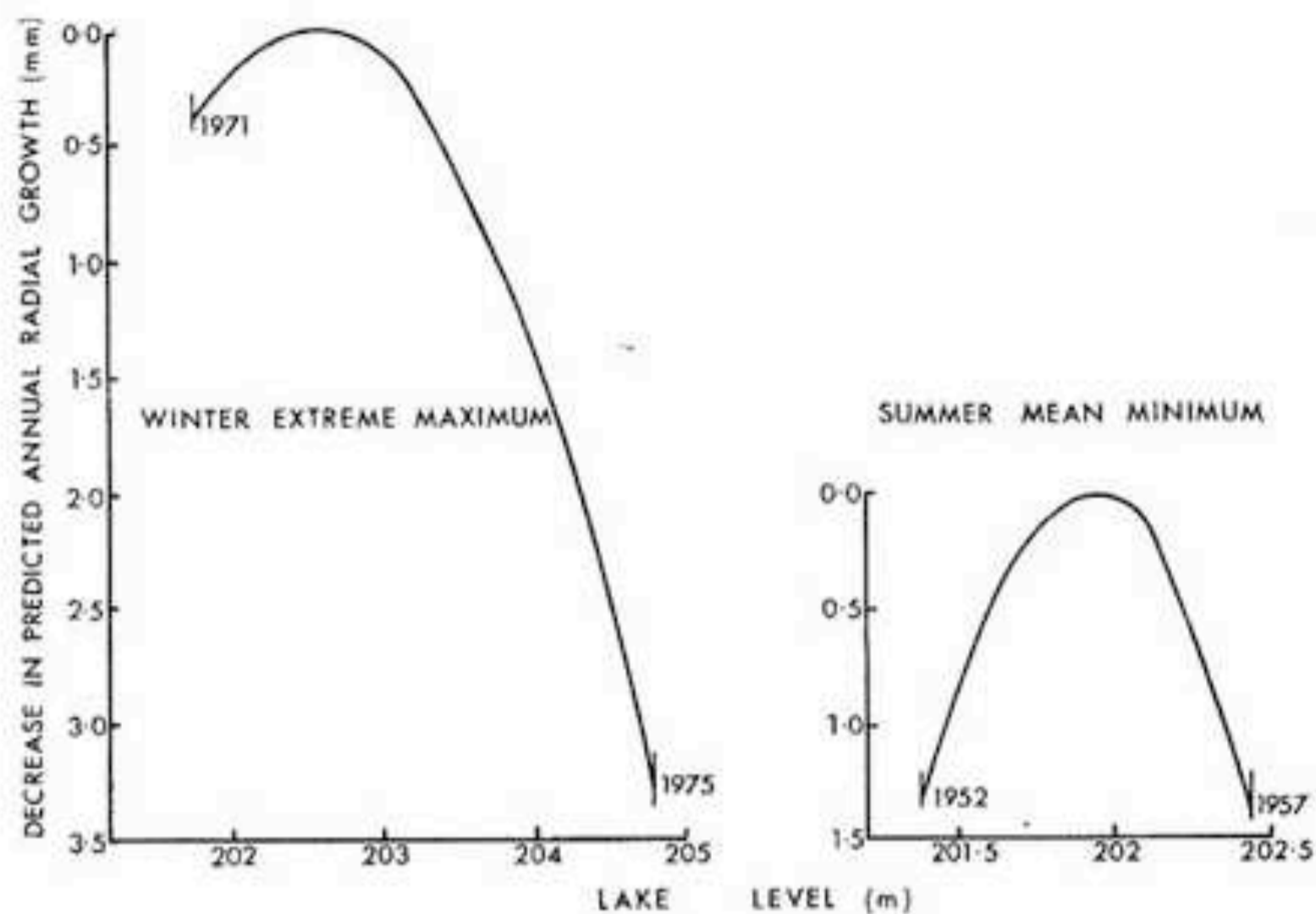


FIGURE 5. Fitted curves from the model in which Te Anau lake levels for each of the last 26 years were related to mean widths of growth rings in silver and mountain beech trees from the lakeshore. "Summer" (September-February) and the preceding "winter" (March-August) lake levels were both included in the model. The curves are plotted only within the range of lake levels observed (Fig. 4) and only the years in which those extremes occurred are indicated. Summer and winter lake levels together accounted for 46% of the annual variation in ring width.

CONTINUING MORTALITY

A resurvey in May 1970 of the 62 affected silver beech trees that were tagged in July 1976 in the Worsley Arm of the lake revealed that only 3 of 16 trees that previously had been partly dead showed no further deterioration. In addition a further 62 trees in the vicinity of those tagged were noted as being either partially (51) or completely (11) dead at this time, indicating considerably delay in response to waterlogging.

DISCUSSION AND CONCLUSIONS

Although plant mortality along the Lake Te Anau shoreline during late spring 1975 was conspicuous only locally on deltas, it is estimated that perhaps 1000 mature trees, mostly silver and mountain beech, but also at least 15 other species including shrubs and herbs, were killed. Despite the complication introduced by differential attacks of pinhole borer on the beeches, these deaths seem clearly related to the unnaturally prolonged flooding which exceeded the tolerance limits of root systems of the 17 or so affected species. With mortality essentially confined to the deltas and its extent apparently related to the texture of the deltaic sediments, direct inundation probably was not the single causal factor.

Retention, for at least 7 months, of the dead leaves on the initially killed beeches is indicative of

physiological stress, probably wilting, which prevented activity of the abscission layer and hence leaf fall. By contrast, beech trees that survived longer and died during late autumn shed their leaves more rapidly, ahead of the spring-killed trees. It is well established that waterlogging of soil can cause changes in a plant's water relations, particularly a reduction in transpiration and even wilting through increased resistance of roots to water flow (Kramer and Jackson, 1954, Kramer, 1969). In beeches, the alternatives—retention of wilted foliage or leaf fall—have been related to the loss of conducting tissue; if the onset of moisture stress is rapid, as when trees are felled in summer or following some platypus attacks, leaves rapidly turn brown without yellowing and are retained (Milligan, 1972). In the case of the Te Anau mortality, Milligan (pers. comm.) suggests that two factors may be involved—rate of death of the roots and rate of spread of the *Platypus*—transmitted pathogen—since both *Nothofagus* and *Weinmannia* are known to be susceptible to this sapwood pathogen.

In the statistical model the dependent variate (dying versus living) was a 2-state variate, so that the analysis can be regarded as the finding of a discriminant function to predict from the elevation, borer class, species, location and live/dead tree pair, which of each pair of beech trees should have lived and which should have died. The model made this prediction correctly in 86 per cent of the pairs (equal-chance pairs were scored as half correct). Therefore, although the whole model was not significant, possibly partly because of the difficulty of getting a good fit to a 2-state dependent variate and partly because of the inclusion of non-useful predictors in the model, the model was able to correlate death with the factors examined. When all the interactions between elevation, borer and species were eliminated from the model the residual sum of squares increased only very slightly (1.13, the mean square being less than the error). Therefore any effects of elevation and borer did not interact and were the same in both species. When elevation was removed from the latter model the increase in the sum of squares was not significant due to a shift in the estimated effects on the removal of the interactions. The percentage of correct predictions of death decreased to 80. This percentage was unchanged as expected, with *only* elevation in the model as a predictor and the difference from the 50 per cent correct, expected on a random basis, confirms the significance of the elevation effect noted earlier. Removing borer from the no-interactions model above, had a much larger effect, the residual sum of squares increasing to 24.05 (the increase being significant at $p < 0.001$). Trees with

borer were shown as more likely to die than those with no borer—a cause or effect situation. Trees for which infestation was not known were, as expected, intermediate in this. With elevation eliminated and borer as the sole real predictor, the percentage of predictions correct stayed at 86. This figure is, however, somewhat misleading in that many of the pairs had the same borer state, given an even chance of dying to each member of the pair. Leaving these pairs aside, the borer model predicted death correctly in 95 per cent of the cases (all but one pair). Since even that one incorrect pair was a case where the borer state was unknown for one member, this indicates great predictive power.

The general conclusion from the statistical source then is that death of trees was correlated with (but not necessarily caused by) both the presence of borer and with low elevation, this being so in both species. Nevertheless the statistical model may not be valid for borer since there are three possible associations between *Platypus* and tree death: a) borer may attack trees already dead, e.g. fallen trees or b) attack otherwise healthy living trees, sometimes killing them or c) attack weakened trees thereby reducing their chances of recovery. Clearly the first type of association cannot be predictive since it occurs only after the event. If the second association was operative at Te Anau the implication from these results is that 95 per cent mortality in beech could be expected if a range of densities of *Platypus* attack were induced on a certain range of sizes of silver and mountain beech. Such, however, is contrary to experimental evidence (Milligan pers. comm.).

Infestation of pinhole borer in beech and kamahi along the Lake Te Anau shoreline is considered to have been a secondary effect in that it is unlikely to have been directly responsible for the mortality. *Platypus* is known to attack weakened trees (Milligan, 1972) though vigorous trees sometimes have been preferentially attacked, presumably by differences in either the amounts or composition of the attractants produced by such trees (Milligan pers. comm.). At Te Anau they infested trees with above average diameter growth. It has been established, however, that flooding may render trees susceptible to the attack of certain beetles (Anderson, 1960), particularly if the flooding impairs the root system's ability to take up sufficient water to compensate for transpirational losses (Milligan, 1974). Despite the claims by Milligan (1974) that beech trees only lightly and abortively attacked have succumbed during an ensuing drought without a secondary concurrent attack, it seems clear that the dead trees along the Te Anau shoreline had not been predisposed in this

way. Some dead beech trees, particularly the smaller ones, showed no sign of borer attack.

The significant relationship between dead beech trees and elevation, and the fact that all dead plants were located within a range of elevations where recent floods have been of longer duration than those recorded naturally within the last 37 years, is highly suggestive of causality. Moreover, apart from some continuing mortality in beech, all of the several thousand plants, both woody and herbaceous, obviously died at about the same time, in October-November and only a few of the 17 species involved can be linked with activities of pinhole borer.

Most dead plants are below an elevation of 203.9 m (669 ft). Above this level, duration of submergence did exceed that previously recorded but to a relatively minor extent (Figs 1 and 2). At elevations around 203.0 m (666 ft) and 203.3 m (667 ft), however, submergence times with the 1975 floods were considerably in excess of previous values. In particular, at 203.0 m, where the longest period of continuous submergence recorded between 1932 and 1971 was 53 days, times of 79 days and 76 days were experienced in April-June and August-November, 1975, respectively. Moreover, it is around this level that the deaths have occurred.

It is probable that flooding *per se* was not responsible for the mortality, but that prolonged high water tables following, and perhaps between, flood peaks is the critical factor. This is suggested in that almost all dead trees were on delta sites, sometimes where impoundment of water behind a storm beach occurs and a slow drop in water table after a flood could be expected because of the gentle slope and fine sediments.

The need to provide for adequate drainage of water tables following excursions into the High Operating Range (>202.7 m or 665 ft for L. Te Anau) was incorporated into the Guardians' Guidelines. These were stipulated as minimum intervals in continuous days between consecutive floods of any particular level (see Figs 1 and 2) and were based on the wettest year of the 37 year period of natural record. These minimum intervals were rarely achieved on Lake Te Anau during 1975 but the value by which guidelines were exceeded varies according to how the situation is interpreted. Either *a.* only those days when the lake is continuously above the particular level are counted, or *b.* all days are included if the "minimum interval between floods" for that particular level has not been achieved. The two methods may provide quite different results (cf. Figs 1 and 2) but it would be reasonable to assume that an inadequately drained water table imparts little benefit to a root system

(Scott and Evans, 1955). This suggests that values shown in Figure 2 probably provide the more realistic interpretation. However, values intermediate between those shown in Figs. 1 and 2 may be more appropriate, a possibility that is enhanced by the contrast in plant mortality between the Lake Te Anau and Lake Manapouri shorelines in relation to their respective lake levels during 1975.

The deleterious effects of submergence or prolonged high water tables on plant roots could be lack of aeration for some species but for the more tolerant ones it cannot be this factor alone since free oxygen is normally exhausted from soil within a day of inundation, particularly in the presence of organic matter (Scott and Evans, 1955). Limits for such species are more likely to be set by the ability of their roots to tolerate a series of frequently toxic reduction products that increase with time as the reduction (redox) potential* decreases (Ponnamperuma, 1965).

Death of manuka, however, appears to have been caused directly by flooding. At 202.4 m (664 ft) and 202.1 m (663 ft) the 1975 flood durations did not exceed those previously recorded, but nevertheless some manuka died at these levels. Moreover, the manuka which did succumb tended to be small plants the foliage on which had been completely submerged for substantial periods. For example, plants growing on the Snag Burn delta had a distinct line at el. 203.04 m (666.17 ft) with only dead leaves below and live ones above. Plants wholly below this level were killed. At this elevation submergence times (continuous days) were as follows in 1975: 80 days from 23 March, 30 days from 2 August, 16 days from 20 September, 28 days from 26 October. Thus although root systems of manuka may be tolerant of floods of about 272 days duration as suggested by Johnson (1972b) survival appears more likely to depend on the period of foliage submergence. Experimental confirmation of this is provided by Craig (1976) who compared survival of manuka seedlings when either wholly submerged or with only their root systems inundated, both in stationary and running water. Plants not only survived but made appreciable growth in flooded anaerobic soil that after 90 days had developed a redox potential of minus 400 mV. This corresponds with the reduction of sulphate to sulphide (Ponnamperuma, 1965). Plants fully inundated in running water remained alive after 100 continuous days whereas death occurred after about 70 days in plants fully submerged in

stagnant water in which the blue green alga *Anabaena spiroides* Klebhan became abundant. Following completion of Craig's study, however, all plants that had been fully submerged in running water soon died. At this time those plants which previously had only their roots submerged and which had made up to 20 cm of stem growth were more deeply inundated in running water, submerging c. 6 cm of stem. Within four months of this treatment there was obvious inflation of the submerged portions of the stems. Microscopic examination of these revealed two pronounced zones of aerenchyma that had been produced by the two most recently differentiated of the deep-seated cork cambia. Above the water line each cork cambium had produced, in addition to a single layer of suberised cork cells (which was also present below the water line), a double layer of non-suberised living parenchyma cells. Development of aerenchyma in submerged parts of stems has been reported in other species with the suggestion that it is the response of a normal phellogen (cork cambium) to some factor of the aquatic environment (Sculthorpe 1967, p. 66). A pronounced development of such aerenchyma is obviously what has been reported as "inflated, highly porous bark at and below the soil surface" in manuka from permanently waterlogged sites (Mark and Smith, 1975), and is undoubtedly what accounts for the ability of this remarkably tolerant species to cope with such conditions. Manuka is obviously more tolerant of flooding than many bottomland woody species (Hosner, 1958). Apparently even-aged stands of manuka around the Fiordland lakes (Johnson, 1972b) may be related to periodic mortality of establishing stands, caused by total submergence during periods of exceptionally high lake levels.

Provided mortality does not continue along the Lake Te Anau shoreline, losses to date, although ecologically significant and obvious in several areas to the casual observer, have made a relatively small impact on the shoreline environment. More important is its indication of the vulnerability of the lakeshore forest and scrub communities to unnaturally prolonged high lake levels and its direct confirmation of flood tolerance limits predicted earlier using indirect methods of assessment (Johnson, 1972b).

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* The reduction (redox) potential of a chemical system is a measure of the tendency for reduction reactions to occur.

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