NOTES ON THE INFLUENCE OF DROUGHT ON THE BUSH REMNANTS OF THE MANAWATU LOWLANDS

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SUMMARY: The data of Atkinson and Greenwood (1972) on drought damage to trees in 1969-70 in two bush patches in the Manawatu district are reassessed, and an index of drought susceptibility based on their data used to classify species into three categories of susceptibility. The results of this categorisation are compared with independent data on the effects of the 1972-73 drought on the nearby bush remnant at Ashhurst Domain. The behaviour of species in all three bush patches is shown to be similar. Comparison is also made with scanty data from other bush remnants, and with the upper altitudinal limits of the species in each category. The results suggest that the different tree species involved have intrinsically different susceptibilities to water stress, which partially explains why in nature they are sorted into hydrologically different situations. The potential application of knowledge on the drought susceptibility of species to reserve management on the one hand, and to past climatic reconstruction using dendrochronology and population structure on the other, is pointed out.

INTRODUCTION

With the upsurge of interest in the recent history of our climate, and in particular the numerous demonstrations that quite significant climatic changes have occurred during the lives of many forest trees living today, the plant ecologist will perhaps begin to pay more attention to the historical climatic or climate-related factors which have influenced the present composition of forest stands. Although this approach has a venerable history in New Zealand (e.g. Holloway, 1954), its full application has been hindered by lack of adequate dating for events hundreds of years in the past, by insufficient knowledge of the population dynamics of the species involved, and, related to this, by uncertainty about the ways in which forest communities as a whole respond to extreme climatic events or secular changes. The first of these inadequacies will probably be overcome by advances in dendrochronology, and information on the population dynamics of individual species is gradually accumulating (e.g. Wardle, 1970, June and Ogden, 1975.) In the field of vegetation dynamics there are very few data, yet it is in this field that information is urgently needed if sound long-term management strategies for forest reserves, national parks etc., are to be implemented.

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The present composition and structure of both *Podocarpus* and *Nothofagus* dominated forest stands has been attributed in part to the climatic conditions (the "little Ice Age") occurring between 1600-1800 AD (see, e.g., Wardle, 1963; Park, 1971; Ogden, 1971; Salinger, 1975). If, in general, present forest composition is in part a function of past climate, then future composition will be influenced by the marked secular increase in temperature which has been occurring throughout New Zealand since c. 1935 (Salinger and Gunn, 1975). Rainfall during this period has shown no significant variation (Salinger and Gunn, 1975). Any tendency towards increased dryness will have its main effect on small isolated bush remnants, because "drying of the forest floor is a vital factor militating against the survival of many species" in such situations (Esler, 1962). If the processes of vegetation change occurring in small remnant bush patches can be adequately documented, and if the climatic factors can be separated from the anthropogenic ones, then information of value to reserve management in a wider context is almost sure to be obtained. Documentation of the effects of drought, or other extreme events, is particularly valuable because it is during the extremes that otherwise imperceptible secular changes become concentrated and quantifiable.

Vegetation change associated with drought occurs because certain species are more susceptible to drought than others, just as changes in composition resulting from browsing by introduced mammals occurs through differential palatability*. Depletion or extinction of certain susceptible species may be followed in subsequent non-drought years by expansion or invasion of more tolerant species. Unfortunately the degree of drought susceptibility of a species cannot be determined simply by scoring the apparent damage it suffers in a particular drought, because susceptibility must be assessed on a time scale similar to the generation time of the population. For instance, if the drought's primary effect is to increase seedling mortality, then species with annual seed production and abundant seedlings will have a higher probability of long-term survival than species with few seeds or seedlings which require conditions for germination or establishment that are not fulfilled annually, despite the much greater *apparent* damage to the former species. Also, a ranking of species in terms of drought susceptibility derived from one area will almost certainly not apply to all situations in which some of these species occur. Just as the relative growth rates of different tree species change according to site conditions (see, e.g. Cameron, 1959) so that a species which is a fast growing dominant in one forest type may be a slow growing subordinate in another, so also will other physiological characters, such as drought resistance, vary in their phenotypic expression according to habitat conditions. Also, it seems likely that in widespread species, particularly those which span a broad altitudinal range, there will be clines of drought resistance, so that different populations of the same species may differ in their ability to withstand extreme drying. Finally, one has to remember that the present distribution of a species may be in part determined by the history of earlier droughts.

These considerations led Atkinson and Greenwood (1972) to conclude that it was not possible to use their data—on observed damage to plants in the 1969-71 drought in two bush remnants in the Manawatu lowlands—to rank the species in order of drought tolerance. This paper, in calling for more attention to be paid to this question, reassesses that conclusion. For comparison, data on the effects of drought in 1973 at Ashhurst Domain (Manawatu district) are presented, and reference made to historically recorded vegetation changes in a similar bush patch and to the altitudinal limits of the species in the nearby mountains.

* In practice, of course, these two causes of change are often confounded.

RESULTS

1. A reassessment of the data in Tables 2 and 3 of Atkinson and Greenwood (1972).

Table 2 of Atkinson and Greenwood (1972) comprises a list of species from different sites within Bledisloe Park, Palmerston North, classified according to size classes and according to the degree of drought damage recorded in 1969-70. The drought damage classes recognised were:

- U plant apparently unaffected
- D many leaves drooping or affected in some other way by drought
- W all leaves wilted, but green foliage still present; with trees and shrubs, death of branches was sufficient to alter shape of crown
- X no green foliage, plant apparently dead.

Table 3 of Atkinson and Greenwood (1972) records the same data for species from Keeble's Bush, Manawatu District.

If for any plant species, irrespective of size-class and site, the number of individuals showing severe drought stress (W and X in Table 2 of Atkinson and Greenwood) is expressed as a proportion of the total number of individuals of the species observed, an "index of drought susceptibility" is obtained. This index varies from 0, where no individuals were placed in the W and X columns of Table 2, to 1.00 where all the individuals were in these two columns. Thus, for the drought resistant *Alectryon excelsus* the index is 0 in both patches of bush studied, while for the susceptible *Beilschmiedia tawa* the index is 0.67 for Bledisloe Park and 0.92 for Keeble's Bush. The absolute value of this index will of course vary with the severity of the drought in which the observations are made, but nevertheless it allows the species to be ranked in order of observed damage. For Bledisloe Park the mean index for the 33 trees and shrubs listed is 0.19, for 9 woody climbers it is 0.35 and for 15 ferns it is 0.53. For Keeble's Bush the mean index for 16 trees is 0.24 (Table 3 of Atkinson and Greenwood, excluding *Cyathea dealbata*). While these results suggest that, in general, ferns show more signs of drought stress than woody climbers which in turn show more stress than trees, they do not necessarily tell us anything about the order in which the groups might become extinct in any bush patch.

Taking indices of drought susceptibility derived from the data in Tables 2 and 3 of Atkinson and Greenwood it is possible to classify the trees and shrubs (and *Cyathea dealbata*) into three broad categories.

Category 1 Plants placed only in classes U and D by Atkinson and Greenwood, therefore with a drought susceptibility index of 0. ("Resistant")

Category 2 Plants with more individuals in classes U and D than in classes W and X, and therefore with a drought susceptibility index of less than 0.5 ("Intermediate")

Category 3 Plants with more individuals in classes W and X than U and D, and therefore with a drought susceptibility index of from 0.5 to 1.0. ("Susceptible")

ately) and 'P' <0.01. A second analysis in which the first five species in the list (tied ranks) were amalgamated and the degrees of freedom consequently reduced from 10 to 6 gave 'R' = .708, 't' = 2.456 (approximately) and 'P' <0.05. Although the data are barely sufficient for confidence, the results do indicate a significant agreement between the two rankings. I conclude that, with regard to drought susceptibility, species generally behave similarly in the two areas. In view of the proximity of the two bush patches, their similar climatic histories, soils etc., this conclusion is, perhaps, not surprising.

TABLE 1. *Classification of trees and shrubs from Bledisloe Park and Keeble's Bush (Tables 2 and 3 of Atkinson and Greenwood, 1972) according to drought susceptibility.*

Category 1 Resistant	Category 2 Intermediate	Category 3 Susceptible
Alectryon excelsus*	Brachyglottis repanda	Aristotelia serrata
Coprosma robusta	Coprosma australis	Beilschmiedia tawa*
Cordyline australis*	C. areaolata	Cyathea dealbata*
Corynocarpus laevigatus	Elaeocarpus dentatus*	Dacrydium cupressinum
Elaeocarpus hookerianus	Hedycarya arborea	Geniostoma ligustriolium
Griselinia lucida	Hoheria sexstylosa*	Macropiper excelsum
Hebe stricta	Knightia excelsa**	Podocarpus dacrydiodes
Leptospermum ericoides	Melicope simplex	Schefflera digitata
Metrosideros robusta	Melicytus ramiflorus*	
Myoporum laetum	Neopanax arboreum	
Myrsine australis*	Paratrophis microphylla	
Nestegis cunninghamii	Pittosporum eugenioides	
N. lanceolata	P. tenuifolium	
Pennantia corymbosa	Pseudopanax crassifolium**	
Podocarpus spicatus*		
P. totara*		
Sophora microphylla		

Note: The 12 spp. recorded for both areas are indicated by asterisks. A single asterisk (*) indicates that the species was placed in the same category in each area. A double askerisk (**) indicates that the species was placed in different categories in the two areas: *Knightia excelsa* in Category 1 in Bledisloe Park and 2 in Keeble's Bush, *Pseudopanax crassifolium* in Category 1 in Bledisloe Park and 3 in Keeble's Bush. Nomenclature throughout follows Allan (1961).

The results of this classification are given in Table 1.

Of the 12 species recorded in both Bledisloe Park and Keeble's Bush, 10 were placed in the same category in both areas; the 12 species are ranked according to their drought susceptibility indices in both areas in Table 2. These data were analysed using Spearman's rank correlation coefficient ('R') and the approximate 't' test (see, e.g. Smith 1967, Moroney, 1956). The first analysis, using the data in Table 2, gave 'R' = 809, 't' = 4.350 (approxim-

2. Comparison with data from Ashhurst Domain in 1973

Relevant rainfall data are given in Table 3. These indicate that the 1972-73 drought commenced earlier than that in 1969-70, but overall was of a comparable severity.

The Ashhurst Domain bush remnant is partly situated on the flat of the Pohangina River, and partly on the terrace above (grid reference N32

2442). Both areas were traversed on 10 March 1973 and the different species classified according to the degree of drought damage they showed. A species was placed in one or more classes depending on the amount of variation in degree of damage shown by

TABLE 2. *Drought susceptibility indices and ranking of species in common between Bledisloe Park and Keeble's Bush.*

Species	Index (and rank) in Keeble's Bush		Index (and rank) in Bledisloe Park	
Alectryon excelsus	0	(3)	0	(4)
Cordyline australis	0	(3)	0	(4)
Myrsine australis	0	(3)	0	(4)
Podocarpus spicatus	0	(3)	0	(4)
P. totara	0	(3)	0	(4)
Elaeocarpus dentatus	0.25	(6.5)	0.20	(9)
Knightia excelsa	0.25	(6.5)	0	(4)
Hoheria sexstylosa	0.36	(8)	0.13	(8)
Melicytus ramiflorus	0.40	(9)	0.47	(10)
Pseudopanax crassifolium	0.50	(10)	0	(4)
Cyathea dealbata	0.64	(11)	0.50	(11)
Beilschmiedia tawa	0.92	(12)	0.67	(12)

TABLE 3. *Rainfall data (mm) for Palmerston North (E05363; DSIR) for the summers of 1969-70 and 1972-73 up to 10th March. (Data supplied by the New Zealand Meteorological Service).*

	1969-70	1972-73	Mean 1941-70
November	33	29	79
December	93	40	104
January	27	50	84
February	9	16	69
March 1-10	1	17	24
TOTAL	163	152	360

different individuals. No counts were made. The results are given in Table 4. The slightly different classification system used means that the data in this table cannot be statistically compared with the results of Atkinson and Greenwood. However, by grouping the species certain general comparisons can be made.

1. Species confined to lower terrace. *(Beilschmiedia tawa; Coprosma australis; Elaeocarpus dentatus; Geniostoma ligustrifolium; Griselinia lucida; Hedycarya arborea; Knightia excelsa; Laurelia novae-zelandiae; Pittosporum eugenioides; Schefflera digitata).*

Of the 10 species found only on the lower terraces 3 fall into drought susceptibility Category 3, 5 into Category 2, and only 2 into Category 1. One of these is the epiphytic *Griselinia lucida* while the other, *Laurelia novae-zelandiae,* was recorded as a single tree only by Atkinson and Greenwood and is only provisionally assigned to this category. Thus the species confined to the lower terrace or not recorded from the upper terrace are predominantly those which show intermediate to marked susceptibility to drought.

2. Species confined to the upper terrace. *(Brachyglottis repanda; Coprosma areolata; Leptospermum scoparium; Melicope simplex; Myoporum laetum; Myrsine australis; Myrtus obcordata; Olearia paniculata; Pennantia corymbosa; Pittosporum tenuifolium; Podocarpus spicatus).*

Of the 11 species in this group, 2 were not recorded by Atkinson and Greenwood, 4 fall into drought susceptability Category 2, and the remaining 5 fall into Category 1. Thus the species apparently confined to the upper terrace are predominantly those which are drought resistant according to this categorisation.

Taking these two groups together it is suggested that either the different species show different ecological requirements of an intrinsic nature related to the independently derived drought susceptibility categories, or else that they have become restricted to their particular terrace stations by continued selective mortality at times of severe water stress. (Both possibilities may be true; indeed they differ only in the time scale over which the selective pressures have operated).

3. Species with some individuals classified as dead on the upper terrace. *(Brachyglottis repanda; Coprosma areolata; Hoheria spp.; Macropiper excelsum; Melicope simplex; Melicytus ramiflorus; Myrsine australis).*

Except for *Myrsine australis,* all these species are categorised as intermediate (Category 2) or drought susceptible (Category 3). The fact that they show severe damage on the upper terrace apparently indicates that this station was suffering from a rather severe drought. The fact that species with intermediate susceptibilities were severely damaged on the upper terrace may be in agreement with the observation that the most susceptible species were absent from this terrace and confined to the lower areas.

4. Species classified as showing no more than mild wilting on the upper terrace. *(Alectryon excelsus; Corynocarpus laevigatus; Leptosper-*

mum scoparium; Myrtus obcordata; Paratrophis microphylla; Podocarpus spicatus; P. totara).

Five out of the 7 species in this group belong to drought susceptibility class 1. One was not recorded by Atkinson and Greenwood and the remaining one falls into Category 2. Thus this group of species, showing the most pronounced drought resistance at Ashhurst Domain in 1973, agree well with the most drought resistant species derived from the independent data from Bledisloe Park and Keeble's Bush.

3. Comparison with historically recorded changes in species composition of other bush remnants of the Manawatu lowlands.

An attempt was made to correlate the drought susceptibility categories given in Table 1 with the survival of species in Kitchener Park, a bush remnant

TABLE 4. *Data on drought effects on trees and shrubs at Ashhurst Domain on 10 March 1973. Drought susceptibility categories taken from Table 1.*
Key to drought damage classes:

1. No damage apparent.
2. Mild damage (a few dead leaves and/or leaves slightly wilted).
3. Severe damage (dead leaves associated with severe wilting).
4. Probably dead (all leaves brown and dried).
nr. Species not recorded.

Species	Drought susceptibility category* (Table 1)	Drought damage classification from upper terrace (Domain)	from lower terrace (Pohangina river flat)
Alectryon excelsus	1	1, 2	1, 2
Beilschmiedia tawa	3	nr	1, 2
Brachyglottis repanda†	2	3, 4	nr
Coprosma areolata	2	3, 4	nr
C. australis	2	nr	1, 2, 3
Corynocarpus laevigatus	1	1, 2	1, 2
Elaeocarpus dentatus	2	nr	1
Geniostoma ligustrifolium	3	nr	1
Griselinia lucida	1	nr	1
Hedycarya arborea	2	nr	1, 2
Hoheria spp (?populnea)	(2)	3, 4	1, 2
Knightia excelsa	2	nr	1
Laurelia novae-zelandiae	nr	nr	1, 2
Leptospermum scoparium	(1)	1	nr
Macropiper excelsum	3	3, 4	1, 2
Melicope simplex	2	2, 3, 4	nr
Melicytus ramiflorus	2	3, 4	1
Myoporum laetum	1	2, 3	nr
Mrysine australis	1	3, 4	nr
Myrtus obcordata	nr	1, 2	nr
Olearia paniculata	nr	3	nr
Paratrophis microphylla	2	1	1
Pennantia corymbosa	1	3	nr
Pittosporum eugenioides†	2	nr	1, 2
P. tenuifolium	2	2, 3	nr
Podocarpus spicatus	1	1	nr
P. totara	1	1, 2	1
Schefflera digitata	3	nr	1

* Figures in parentheses based on related species from Table 1.

† Species recorded only on the steep slope connecting the two terraces, and classified as "upper terrace" or "lower terrace" depending on position on slope.

in the Manawatu District which has been reported on by Esler (1962, and unpublished report to Fielding Borough Council, May 1967). An exact correspondence between the drought susceptibility of a species—as indicated by the degree of wilting of its leaves etc.—and its survival in a bush remnant was not expected, because survival in such situations depends on many factors, including the quantity of viable seed produced, seedling characteristics, palatability to browsing animals, etc. Also, because the original list given by Allan (1924) was incomplete and the exact area referred to was not given, it is impossible to ascertain for sure whether the drought susceptible species have in general suffered a greater decline in numbers than the resistant species. The latter are generally more frequent at Kitchener Park than are species of intermediate susceptibility (Category 2), but both categories have shown a decline in abundance between 1945 and 1967 (Esler, unpublished report to Feilding Borough Council, May 1967). The drought resistant *Alectryon excelsus* and *Pennantia corymbosa*, and the intermediate *Melicytus ramiflorus* are regarded by Esler (1962) as species which maintain themselves in the bush remnants of the Manawatu lowlands "more readily than most others". The ferns, requiring moist conditions for their gametophytes, have shown a marked decline in the bush remnants. At Kitchener Park 25% of the species of ferns referred to by Allan have now disappeared, including *Cyathea dealbata* (Category 3). (Esler, unpublished report to Feilding Borough Council, May 1967). Apart from *C. dealbata* none of the species listed in Category 3 have become extinct over the last 50 years at Kitchener Park, but considering the longevity of most of these species this is perhaps not surprising. However, *Macropiper excelsum* (Category 3) and *Brachyglottis repanda* (Category 2) have increased. Conclusions are difficult because the past influence of browsing animals, including cattle, may have had a far greater effect than droughts.

4. Comparison with upper altitudinal limits of species.

The Ruahine and Tararua Ranges border the Manawatu Plain to the east. In general, with increasing altitude in these mountains average rainfall increases and temperature declines. It seemed possible therefore that the more drought resistant species listed in Table 1 might be species adapted to lower elevations and the susceptible species might be montane plants near the lower limits of their altitudinal distributions. This question was examined by listing the highest recorded altitude of occurrence in the Ruahine and Tararua Mountains of all the species in each category in Table 1 and performing an analysis of variance on the data. Altitudinal data were obtained for the Ruahines from Ogden (1971, and subsequent unpublished revision) and Aston (1913) and for the Tararuas from my unpublished records from Mt Kapakapanui. Although the analysis of variance showed no significant differences between the upper altitudinal limits of the species in different categories, it is of interest to note that the mean upper limit for Category 1 plants is 646 ± 40m and for Category 2 is 767 ± 55m ('t' for comparison of means = 1.807, with 29 degrees of freedom 'P' $<.10$). In general it appears that the drought resistant species listed in Table 1 are predominantly lowland in their occurrence, while the more susceptible species show no clear correlation with altitude. This conclusion corresponds with field experience elsewhere (I. Atkinson, pers. comm.).

DISCUSSION AND CONCLUSIONS

This analysis suggests that the different tree species involved have intrinsically different susceptibilities to water stress. Such differences may partially explain why the different species are sorted into different ecological situations, such as upper and lower terrace, but it does not seem to explain the overall altitudinal gradation in forest composition from the Manawatu lowlands to the montane forests of the adjacent ranges. It is important to stress that the relative susceptibilities listed in Table I will almost certainly not apply to all situations in which combinations of some of these species occur. The bush patches reported upon here are all in the same climatic region and situated on similar soils, so that the general agreement between them is reassuring but not surprising. However, the type of information presented in Table 1, albeit preliminary and imprecise, could be used to help in the assessment of the degree of deterioration shown by any particular bush remnant, information perhaps of value in determining priorities for conservation. The extension of this type of semi-quantitative observation to other areas of New Zealand might allow a more general categorisation to be drawn up, which could be put to more practical application.

A further use of such a categorisation would be in the choice of species for reconstruction of past climatic or hydrological conditions using dendrochronology (see, e.g. Fritts, 1971). For example, from Table 1, it might be suggested that when growing on the same site susceptible species such as

Podocarpus dacrydioides and *Dacrydium cupressinum* will reflect in their annual ring width variations the past history of droughts more clearly than resistant species such as *Podocarpus totara* and *P. spicata*. (However, it could be argued that susceptibility arises from inability to restrict annual ring growth in which case the situation would be reversed and resistant species be the best indicators). Although this hypothesis requires testing, it does seem safe to conclude that quantitative information on drought susceptibility could be used both in a predictive sense to postulate future changes in species composition, and, using population structures and annual ring width variability, retrospectively, to reconstruct past climatic conditions.

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