

EXTREME CLIMATIC FLUCTUATIONS AS A CAUSE OF FOREST DIEBACK IN THE PACIFIC RIM

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Abstract. An overview of forest diebacks in regions of the Pacific Rim strongly implicated extreme climatic fluctuations as a cause of dieback in the absence of significant acidic deposition and O₃ pollution. There was strong circumstantial evidence that extreme moisture fluctuations had incited cavitation injury on *Eucalyptus*, *Metrosideros* and *Nothofagus* species with recent dieback.

The onset and intensification of crown dieback on *Metrosideros* in Hawaii related directly to the incidence of extreme rainfall followed by prolonged (2 to 4 weeks) clear, hot, dry weather. Research needs to substantiate the role of an irreversible cavitation dysfunction of the xylem as a mechanism of persistent crown dieback were discussed.

1. Introduction

The Pacific Rim diebacks offer a unique opportunity – serving as a natural laboratory in which to investigate the primary cause of forest dieback in the absence of significant levels of regional pollution.

They also pose a dilemma in that some researchers have argued that diebacks in the Pacific Region have features that are symptomatically different from those of eastern North America and central Europe: they affect overstory trees only, are confined to a single species at each location, and result from natural stresses within the forest, notably cohort senescence (McLaughlin, 1985). Manion (1985) cautioned that in the absence of more adequate documentation of the diebacks, such conclusions regarding the Pacific Rim region may be premature or mistaken. Auclair *et al.* (1990) noted striking parallels between forest dieback symptoms in the Pacific Northwest and those in eastern North America. Moreover, both regions had a highly anomalous winter thaw/freeze in the onset years of dieback. Massive cavitation typified the diebacks in the Northern Hardwoods, and on the basis of inter-regional comparisons, Auclair *et al.* (1992) hypothesized that extreme climatic fluctuations may have incited diebacks through dysfunctional cavitation more generally.

Is it possible that massive cavitation incited by extreme climatic fluctuations is a common thread among forest diebacks in regions as geographically and ecologically

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discrepant as Oceania, western and eastern Northern America, and central Europe? If so, what approaches are required to identify such a mechanism?

THE ISSUE

There is much literature evidence indicating that extreme climatic fluctuations play a significant role in the forest diebacks of the Pacific Rim. (a) With few exceptions (eg Batcheler, 1983), water stress has been implicated as a primary or secondary factor in all the major diebacks of the region. (b) Extreme weather events such as flooding, heavy rains, drought, or wet/dry oscillations are common in the region and have been related to the onset of *Eucalyptus* diebacks in Australia (Davison, 1988; West, 1979; White, 1986; Wylie and Bevege, 1980) and of dieback on *Nothofagus* in New Zealand (Jane and Green, 1986), and (c) climatic 'instability' remains a central focus of the prevailing hypothesis on the *Metrosideros* dieback of Hawaii (Mueller-Dombois, 1980, 1985, 1986).

Despite the recognized importance of climate, evidence of a mechanism from carefully done climatic analyses is still lacking (Mueller-Dombois, 1983). Both Doty (1982, 1983) and Evenson (1983) concluded that the *Metrosideros* dieback of the 1960 and 1970 decades was not correlated with either drought or exceptionally wet years. Their analyses used monthly or annual values and important climatic events such as short term fluctuations related to storm or seasonal anomalies remain to be fully investigated (Mueller-Dombois, 1985).

OBJECTIVE

The specific objective of this paper is to test the hypothesis proposed recently as a general framework for explaining forest diebacks (Auclair *et al.*, 1992):

Hypothesis

Forest diebacks are incited by extreme moisture and/or freezing fluctuations that result in injury to tree conductive systems by irreversible cavitation.

2. Methods and Data

DEFINITION

There remains a large conceptual gap between early research (1940-1970) focused on climate as a cause of forest dieback and the current focus on air pollution. In this proposal we use *forest decline* to refer to a progressive reduction of productivity and health caused by a potentially wide range of factors, acting individually or interactively. *Forest crown dieback*, when persistent and region-wide, is perceived to be one specific (and commonly extreme) type of forest decline. All have the following essential features: they are persistent, progressive, and ultimately extend over much of a forest region or subregion; and they show many crown anomalies – early leaf coloration and premature leaf-fall, leaf necrosis, small leaf size, tufting of leaves,

and stem dieback from branch tips inward toward the bole. Mortality of fine roots and reduced radial growth are also characteristic symptoms.

APPROACH

The intent was to scope broadly the role of climate and to examine, in at least one specific case, the possibility that extreme climate fluctuation had resulted in irreversible cavitation leading to dieback.

Regional Overview

An overview of the evidence in published literature and government reports was made of both direct and circumstantial evidence that cavitation injury exists in trees with severe crown dieback in the Pacific region. In-depth case studies of climate were made in each of the three major diebacks of the region, namely on *Eucalyptus*, *Metrosideros* and *Nothofagus*. Auclair *et al.* (1990) had previously reviewed the incidence and origin of forest diebacks in the temperate Pacific Northwest.

Event Analysis

The second step consisted of an 'event analysis' of the *Metrosideros* dieback in Hawaii. This choice had the advantage that the Hawaiian diebacks have a documented history, their distribution and many of the environmental factors have been quantified and/or mapped (Hodges *et al.*, 1986; Jacobi, 1983; Mueller-Dombois, 1985; Mueller-Dombois, 1980). Onset years and progress of the dieback were reconstructed from aerial surveys (Petteys *et al.*, 1975; Hodges *et al.*, 1986) and ground monitoring plots (Jacobi *et al.*, 1988), supplemented where necessary by other descriptive literature. The meteorological conditions during the onset period(s) were reconstructed from daily records of total precipitation and minimum/maximum temperature at Hilo on the island of Hawaii (National Climatic Data Centre, 1990). Continuous meteorological records were available over the 1949 to 1990 period, making possible an analysis of onset events as well as conditions before and during the progress of the dieback.

3. Results and Discussion

REGIONAL PATTERNS

The Pacific Rim diebacks encompassed tropical, subtropical to temperate environments (Figure 1) and included a broad spectrum of angiosperm and conifer forest types (Mueller-Dombois, 1983). Several of the larger diebacks such as that on Alaska yellow cedar (*Chamaecyparis nootkatensis*), the beech (*Nothofagus antarctica*) dieback in Patagonia (Veblen and Lorenz, 1988), and the extensive eucalypt (*Eucalyptus spp.*) diebacks of Australia have not been widely recognized in the recent North American and European literature. In fact, the diebacks both in Alaska (Hennon and Newcomb, 1986; Hennon and Shaw, 1985; Hennon *et al.*, 1987; Shaw and

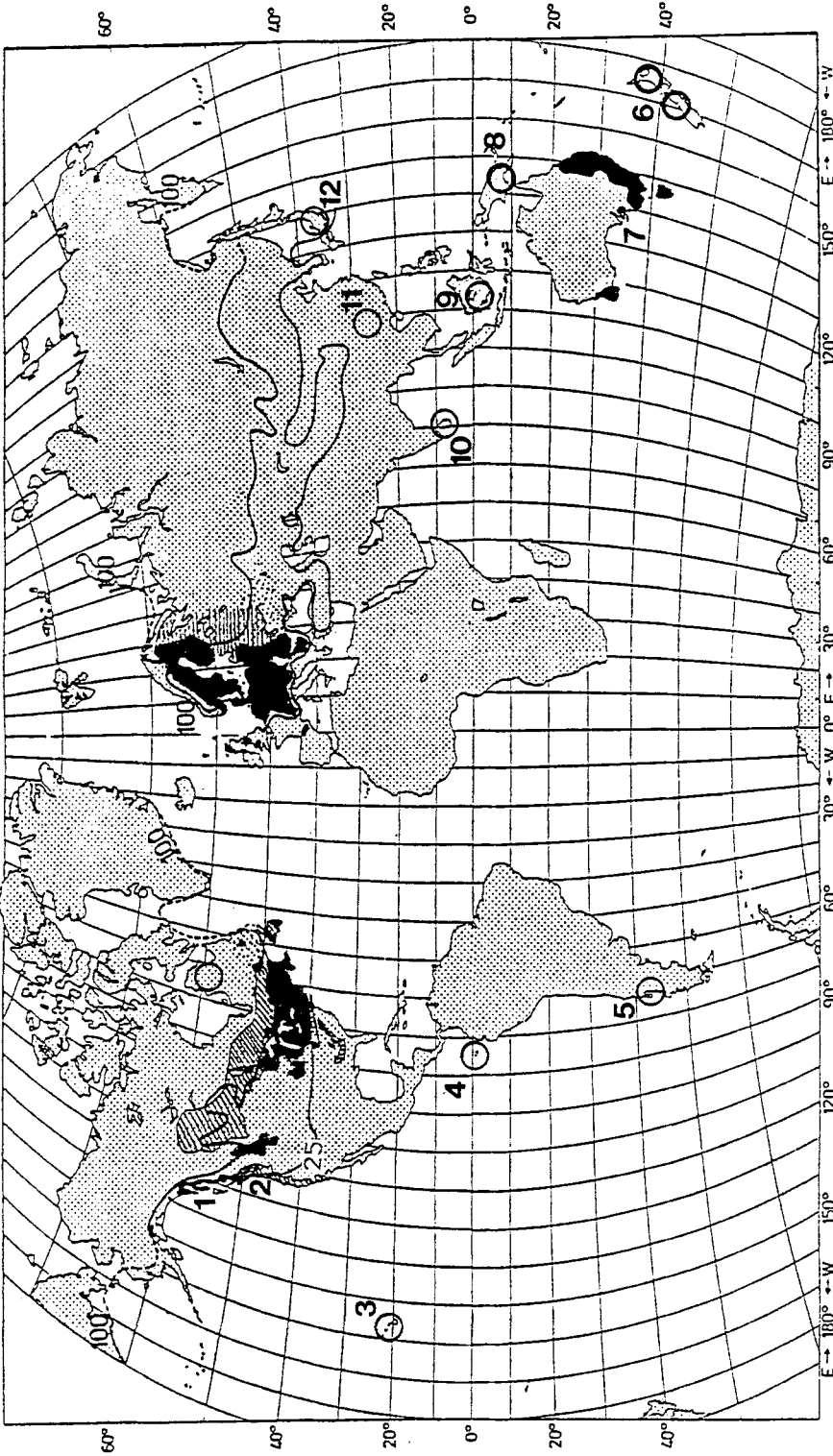


Fig. 1. The global distribution of region-wide, persistent forest crown dieback reconstructed from literature and survey reports. Numbers 1-12 refer to locations of the Pacific Rim listed in Table I. The 25 and 100% isopleths for the probability of 25mm of snowcover on the last day of January are indicated.

TABLE I

Enumeration of the Pacific Rim diebacks; 'lead' species, total number of tree genera and species affected, areal extent, date(s) of onset of the recent and previous episodes, and climatic factors implicated. Long-term climatic changes (T, increase in the hemispheric or global mean annual air temperature; P, a decrease in the regional or local mean annual precipitation; O, unknown) have been distinguished from short-term extreme climatic fluctuations (Type I-V of Table II, parentheses indicating the role of climatic fluctuations is unresolved, the most probable factors being given)

Location	'Lead' species	No. genera	No. species	Extent (Ha)	Onset date	Climatic factors	
						Change longterm	Extreme anomalies
1 Alaska	<i>Chamaecyparis nootkatensis</i>	4	5	90000	1880's	T, P	(V, I)
2 Pacific Northwest	<i>Pinus monticola</i>	13	28	190000	1936	T, P	V
3 Hawaii	<i>Metrosideros polymorpha</i>	3	3	50000	1953 (1875)	P	I, II, (V)
4 Galapagos	<i>Scalasia pedunculata</i>	1	1	(1000)	1983 (1930's)	O	(I)
5 Chile (Patagonia)	<i>Nothofagus antarctica</i>	1	1	(30000)	unknown 1972	P	(IV)
6 New Zealand	<i>Nothofagus menziesii</i>	9	15	(25000)	1946 (1900's)	O	II
7 Australia	<i>Eucalyptus nova-anglica</i>	9	102	425000	1960's (1920's) (1850's)	T, P	I, III, IV (V)
8 Papua New Guinea	<i>Nothofagus pullei</i>	3	4	(5000)	unknown	O	(V)
9 Sarawak	<i>Shorea albida</i>	3	3	12000	1948	O	(III)
10 Sri Lanka	<i>Calophyllum walkeri</i>	2	4	(1000)	1970's	O	(IV)
11 China	<i>Pinus armandii</i>	2	3	6000	1980's	O	(V, VI)
12 Japan	<i>Abies fabri</i> <i>Abies veitchii</i> <i>Abies mariesii</i>	1	2	(10000)	ongoing	O	(V, VI)

Hennon, 1985; Shaw *et al.*, 1987, 1988) and Australia (Bird *et al.*, 1974; Heatwole and Lowman, 1986; Marks and Idczak, 1973; Old *et al.*, 1980) have been studied in-depth and have received considerable local attention.

The pattern now common to regions of the Pacific Rim was for a broad complement of tree species to be affected in addition to a 'lead' species. Over time and over the full areal extent of a large and diverse region many species typically showed crown dieback. It was recognized that small islands with a few, strong dominants were a feature of the Pacific Rim and have resulted in conditions with chronic dieback in monospecific stands (Mueller-Dombois, 1986), the broad potential for dieback notwithstanding. In Australia, 102 species in 9 different genera showed dieback. In the 1960's only the New England peppermint (*Eucalyptus nova-anglica*) showed widespread, chronic dieback; by the mid-1970's at least 6 tree species had developed severe dieback problems and minor occurrences were noted on a larger number. By the 1980 decade dieback had greatly intensified in the New England Tablelands (Heatwole and Lowman, 1986). In New Zealand 15 tree species in 9 genera showed persistent dieback. In addition to dieback on *Metrosideros polymorpha* in Hawaii, dieback affected *Acacia koa*, the second most abundant native tree, and since 1977, *Leucanea leucoccephala* on Oahu and Maui. Over the north temperate forests of China, Japan, and western North America, 28 species in 13 genera showed extensive crown dieback.

The areal extent, severity, and the onset dates were weakly documented in the literature. Onset dates reported indicated that crown dieback had been initiated in most decades of this century; early diebacks had been reported in the 1870 and 1880 decades (Table I). Tree-ring analysis on species with dieback in New Zealand indicated the possibility dieback episodes may have occurred in the North Island montane forests in the 17th (1656) and early 19th (1804, 1861) centuries (Jane and Green, 1983 p. 387).

CASE STUDIES

What evidence was there of an extreme climate-cavitation-dieback link in cases where the role of climate has been studied? Were long-term climate shifts evident?

Eucalyptus Dieback in Australia

There was unequivocal evidence of a cavitation disorder on jarrah (*E. marginata*) in Western Australia. No consistent lesions were observed and no known pathogens isolated in a series of early pathological investigations. Crown dieback on the species was not confined to sites infested by *Phytophthora cinnamomi* (Davison, 1988). The only abnormality noted in anatomical studies was more root xylem with tyloses in dying trees than in unaffected trees (Wallace and Hatch, 1953).

Jarrah was extremely sensitive to waterlogging (Podger, 1967) and dieback was most common in soils with impeded drainage (due to clay or massive laterite) and on low catena such as saddles, valley bottoms, and gully heads. Unlike most woody plants which close their stomata when soil are waterlogged, glasshouse experiments

showed jarrah seedlings continued to transpire; the tap roots embolished (ie cavitated) quickly and were sealed off with tyloses (Davison and Tay, 1985).

In addition to the association of jarrah dieback with water-gaining sites, extensive summer and winter rainfall played a role, presumably by the periodic saturation of all or part of the soil profile. Davison (1988) noted that the several jarrah episodes followed excessively wet winters and unusually dry summers in the late 1940's, the mid 1960's and 1973, and heavy cyclonic rainfall (>200 mm/48 hr) in the late 1950's and in 1982.

White (1986) computed a stress index of rainfall fluctuation (wet weather followed by a period of unusually dry weather) based on the assumption that dieback was initiated by mortality of feeder roots drowned during periods of excessive rainfall; the reduced root/crown ratio was assumed to result in serious water imbalance during dry weather. Using meteorological records for Armidale (1860-1984), he demonstrated a close relationship existed between the stress index and the major intervals of eucalypt dieback on the New England Tablelands of eastern Australia. In addition to root damage, site and rooting habit exacerbated the effects of climatic fluctuations. The most sensitive species, the peppermint gum, was both shallow rooting and occupied poor, thin, heavy clay soils in a climate of fairly high rainfall and infrequent dry weather – making the species particularly vulnerable to periods of drought. White (1986) concluded that climatic perturbations, and those of rainfall in particular, were the primary cause of forest diebacks in Australia. Senescence and attack by defoliating insects were seen to be secondary factors.

There was a high probability that frost and freezing events played an inciting role in the eucalypt diebacks of temperate regions of Australia but there was virtually no experimental evidence of this. Eucalypts were particularly susceptible to cold damage in early stages of growth and during periods of rapid shoot extension; frost damage had been observed to cause leader and whole tree mortality on an extensive scale both in native and in exotic locations (Podger, 1973). Two diebacks, that on *E. delegatensis* in high mountains and plateaux (>760 m) of Tasmania (Hopkins, 1973) and on *E. pauciflora* at timberline in the Snowy Mountains (Slayter, 1976) were strong candidates for frost-induced cavitation damage. In the later case, Slayter (1976) concluded that extensive 'shoot-dieback' was caused by natural radiation frosts associated with periods of clear weather and cold nights in the spring when tissue was no longer winter hardy.

The stress index of wet/dry oscillations in eastern Australia showed a consistent upward trend, 1860 to 1984 (White, 1986). There were also examples of long-term increases in mean annual temperature (Pittock, 1983) and decreased rainfall (Kimber, 1980; Podger, *et al.*, 1980; West, 1979; White, 1986) in regions of eucalypt dieback.

Nothofagus Dieback in New Zealand

Since the mid-1940's montane forests on the North Island of New Zealand have shown severe, episodic dieback on the predominant forest tree species (*N. menziesii*, *N. fusca*, *Beilschmiedia taxa*, *Ixerba brexioides*). The incidence of the dieback related

closely to the distribution of the cloud zone at mid to upper elevation (>550 m), almost continuous soil waterlogging, and periodic drought; the onset of the recent dieback episodes coincided with droughts in 1946 and 1972. Because of poor root development in waterlogged soils and weakly developed leaf resistance to water loss, it was hypothesized that trees grown in these conditions were hypersensitive to even the slightest moisture stress (Jane and Green 1983). Skipworth (1981) and Wardle and Allen (1983) also linked the dieback on red and mountain beech (*N. fusca*, *N. solandri*) on the central North Island and on the South Island to episodic drought.

Of particular note was the possibility of frost or freezing events in the dieback on mountain beech on the south Island in 1973. Although crown breakage by heavy snow was implicated, dieback and mortality was also evident on canopy trees that had escaped the initial damage and the actual mechanisms remained unresolved (Wardle and Allen, 1983). Frost damage was not mentioned. It was noteworthy, however, that Arentz (1988) had implicated frost as a possible trigger in the recent dieback of *Nothofagus* in the central highlands of Papua New Guinea (2400 to 2700 m). A series of frosts between June and October 1972, accompanied by a prolonged drought had caused extensive damage to crops and vegetation in the western and southern highlands. Severe frosts (-5 °C) and accompanying drought had occurred in 1940, 1941, 1949, 1950, 1962, 1971, and 1972, that is, approximately twice per decade (Brown and Powell, 1974). Freezing can be an important factor in cavitation injury (Tyree and Sperry, 1989). Even cold soils (e.g. 5C) without frost may be sufficient to initiate cavitation if the canopy is simultaneously exposed to strong evapo-transpiration demands.

None of the New Zealand studies provided direct evidence of cavitation injury but the extreme forms of water (and possibly freezing) stress were highly suggestive that this kind of disorder may have occurred.

There were no analyses of long-term temperature or precipitation changes in relation to the New Zealand forest diebacks. Steward and Rose (1988) examined deviations from the annual rainfall normal at Hokitika, South Island 1866-1982; although they noted a higher frequency of low rainfall in summer and early autumn (Dec-Apr) since 1930, there was no general indication of a drying trend.

*Dieback of *Metrosideros* in Hawaii*

Although cavitation injury had not been documented in dying *Metrosideros*, there were three lines of circumstantial evidence such injuries may have occurred. First, some work relevant to the question had been done in relation to cohort senescence. Gerrish (1988, 1990) proposed a 'pipe model' based on Huber values (total sapwood volume to leaf mass) to explain declining carbon balance with age. He argued that a reduction of sapwood would have been at the expense of water supply to the crown; he hypothesized that a high hydrological conductivity in sapwood may have been achieved by morphological adjustments in the xylem. He cited Sastrapradja (1965) who had found that the abundance of vessel and tracheid pores in *Metrosideros*

increased significantly from inner, younger wood to the outer, older wood. The key point was that this altered xylem structure increased exponentially the risk to cavitation with age (Zimmermann, 1983); this accorded well with observations that the incidence of dieback was greatest in older cohorts of *Metrosideros* (Mueller-Dombois, 1985).

Second, over 80% of the area in dieback occurred on continuously waterlogged sites (Wetland and Bog Formation Diebacks). An additional 15% occurred on very poorly drained soils (Ohia-Koa and Gap Formulation Dieback). Severe dieback occurred on moderately to well-drained substrates (Ohia Displacement and Pubescent Ohia Dieback) but this comprised only a small percentage (<5%) of the total area (Mueller-Dombois, 1980; Hodges *et al.*, 1986). Soil waterlogging was assumed to have limited root development and result in trees vulnerable to episodic drought.

The possibility of root xylem cavitation (as noted on jarrah in Western Australia) needed to be considered, particularly with regard to sites periodically flooded. It was noteworthy that even the moderate and well-drained sites (Ohia-Koa, Displacement, Pubescent and Dryland Diebacks) experienced periodic soil saturation during heavy rainstorms (Hodges *et al.*, 1986). It was not improbable that a prolonged interval of exceptionally wet weather (eg 2-3 weeks) resulted in sustained soil saturation on these well-drained sites.

Third, a significant feature of the *Metrosideros* dieback zone in Hawaii was persistent cloud and/or fog – a feature creating extreme sensitivity to moisture stress during episodes of dry, bright weather. Petteys *et al.*, (1975) had observed that the incidence of dieback increased with increasing precipitation. The most severe dieback occurred at the mid-elevation on windward slopes where rainfall was generally highest (5000 to 7500 mm, compared to ca 2500 mm at Hilo on the coast).

Mueller-Dombois' (1980) hypothesis that dieback on mature *Metrosideros* was triggered by extreme rainfall or extreme drought was supported by his analysis of monthly rainfall records (1900-1984) at Hilo, Hawaii (Mueller-Dombois, 1986). Nine severe floods and 6 severe droughts had occurred over an 85 yr period. The main dieback period (1954-1984) was especially variable (5 severe floods and 4 severe droughts). Evenson's (1983) analysis of meteorological records over the dieback zone indicated that although mean monthly temperature did not vary greatly, mean monthly and annual rainfall was highly variable. He surmised that unusually wet years contributed to sharp increases in dieback on wet sites, 1965-1977, and to its expansion on dry sites during the droughts of 1958, 1959, and 1962.

There was ambiguity on the perceived role of extreme rainfall (Mueller-Dombois, 1985). (a) Evenson's (1983) climatic analysis and Doty's (1982) study of stream-flow rate for the dieback area in the Hilo watershed (1936-1979) could not substantiate a significant relationship to the onset or progression of the dieback. (b) Extreme climatic disturbances occur repeatedly throughout the 200 to 400 yr life-

span of *Metrosideros* and were not considered as the only cause of stand-level mortality (Mueller-Dombois, 1988 p. 449). (c) There was a clear perception that further analyses of storms and seasonality was essential in addressing meaningfully the issue of climate (Evenson, 1983; Mueller-Dombois, 1985).

The possibility of cold air drainage (Mueller-Dombois, 1988 p. 449) from the high elevations into the dieback locus, i.e. saddle and drainage-impeded sites at mid-elevation, should not be dismissed lightly. Although the volcanic peaks of Mauna Kea and Mauna Loa (3500 m) were periodically covered with snow, no analysis was available of cold or freezing events as a cause of dieback.

A long-term (78 yr) decrease in the annual rainfall was apparent in the dieback area; of 24 stations on the windward, northeast slope of the island of Hawaii, all showed a decrease; the trends at 6 of these stations were statistically significant. The most extreme case involved a 40% reduction 1900-1977, but the overall trend was so small that it was dismissed as biologically meaningless (Mueller-Dombois, 1988 p. 448).

Summary of Dieback Case Studies

There was strong circumstantial evidence of cavitation injury in the forest and woodland diebacks, notably the incidence of extreme, episodic moisture fluctuations. Five of the six more or less distinct types of extreme climatic fluctuations involved acute moisture stresses (Table II). There was also the possibility that inciting frost and freezing events in some montane areas may have initiated dieback, either directly

TABLE II

Classification of extreme climatic anomalies likely to incite cavitation injury leading to forest crown dieback in regions of the Pacific Rim

Type	Climatic anomaly	Description	References
I	Wet-dry oscillation	Unusually heavy rain followed by bright, clear, dry, hot weather	Davison, 1988; Itow and Mueller-Dombois, 1988; Mueller-Dombois, 1986; White, 1986
II	Intermittent high pressure or blocking high	Disruption of typically foggy/cloudy conditions by clear, hot weather	Jane and Green, 1986
III	Extreme rainfall	Flooding involving soil waterlogging	Davison, 1988; Wylie and Bevege, 1980
IV	Extreme drought	Unusual drought and heat	Kimber, 1980; Leaphart and Stage, 1971; West, 1979; Veblen and Lorenz, 1988
V	Acute frost desiccation	Unreasonably warm weather at the times the ground was cold or frozen	Andersen, 1959; Auclair <i>et al.</i> , 1990, 1992; Kohyama, 1988; Pomerleau, 1991
VI	Thaw-freeze or frost	Intense winter thaw-freeze or deep unseasonable frost	Auclair <i>et al.</i> , 1990, 1992; Reich, 1990; Russel, 1965

or through collateral damage. The key stresses among the Australian, New Zealand and Hawaiian forest diebacks were either (a) extreme rainfall followed by dry weather, or (b) the interruption of more or less continuous cloud. (c) In all cases impeded soil drainage was paramount in causing hypersensitivity to drought by reducing root growth, when persistent, or in the development of tyloses in the root xylem when flooding occurred intermittently. The onset of cavitation injury was assumed to have occurred at the time of episodic flooding (as with jarrah) and/or, on trees with reduced root systems, during episodes of elevated evapo-transpiration demands on the canopy (dry, bright weather).

Long-term changes in mean annual temperature and/or precipitation had been documented in 5 of 12 regional diebacks (Table I). The relation between short-term extreme fluctuations and shifts in mean annual temperature or rainfall (Wigley, 1985) remained to be investigated. Where extreme wet/dry oscillations were analyzed, there was a marked trend towards increasing levels of stress in the more recent, warmer decades (White, 1986).

EVENT ANALYSIS OF METROSIDEROS DIEBACK ON HAWAII

Historical Reconstruction

Historical accounts indicated that episodes of dieback had occurred on different islands at different times (Figure 2). Dieback on *Metrosideros* had been observed as early as 1875 (Clarke, 1875) and several reports described episodes on this species early this century on Kauai (Larsen, 1910) and on Maui (Territory of Hawaii, 1907; Lyon, 1909). Mueller-Dombois (1986 p. 232) reported a recent (1977-1983) widespread dieback of *Leucaena leucocephala* on Oahu and Maui.

The current wave of *Metrosideros* dieback on the island of Hawaii was by far the largest and most persistent yet documented in the State. Early, localized incidences had been reported in 1947 (Davis, 1947) and in 1954 (Pettyes *et al.*, 1975), but the main expansion period occurred later. A sequence of aerial reconnaissances showed the extent of dieback, limited to 120 ha in 1954, had increased to about 15,700 ha by 1965, 34,500 ha in 1972 and 50,000 ha in 1977 (Jacobi *et al.*, 1988). According to local residents, the dieback first became noticeable in the early 1960's and had reached its greatest extent by 1974 (Jacobi *et al.*, 1988). A phase of considerable intensification but little expansion followed 1974. Jacobi (1983) observed a great increase in the spread of wetland dieback between 1965 and 1977; the dieback stopped totally in 1977 and had not spread any further in 1981. An aerial survey in 1982 covered a somewhat different and larger area (76,951 ha) and could not be directly compared to the earlier surveys; 41% had severe dieback, 23.7% had moderate dieback, and 35.3% was healthy or had only slight dieback (Hodges *et al.*, 1986). A reassessment of 25 ground monitoring plots over the dieback area in 1986 confirmed that dieback had not expanded since 1977 but that more plots (4 or 16%) were severely or moderately affected; 2 of the 25 plots in 1986 showed some recovery in the form of epicormic branches on the bole and/or at the base of the trunk (Jacobi *et al.*, 1988).

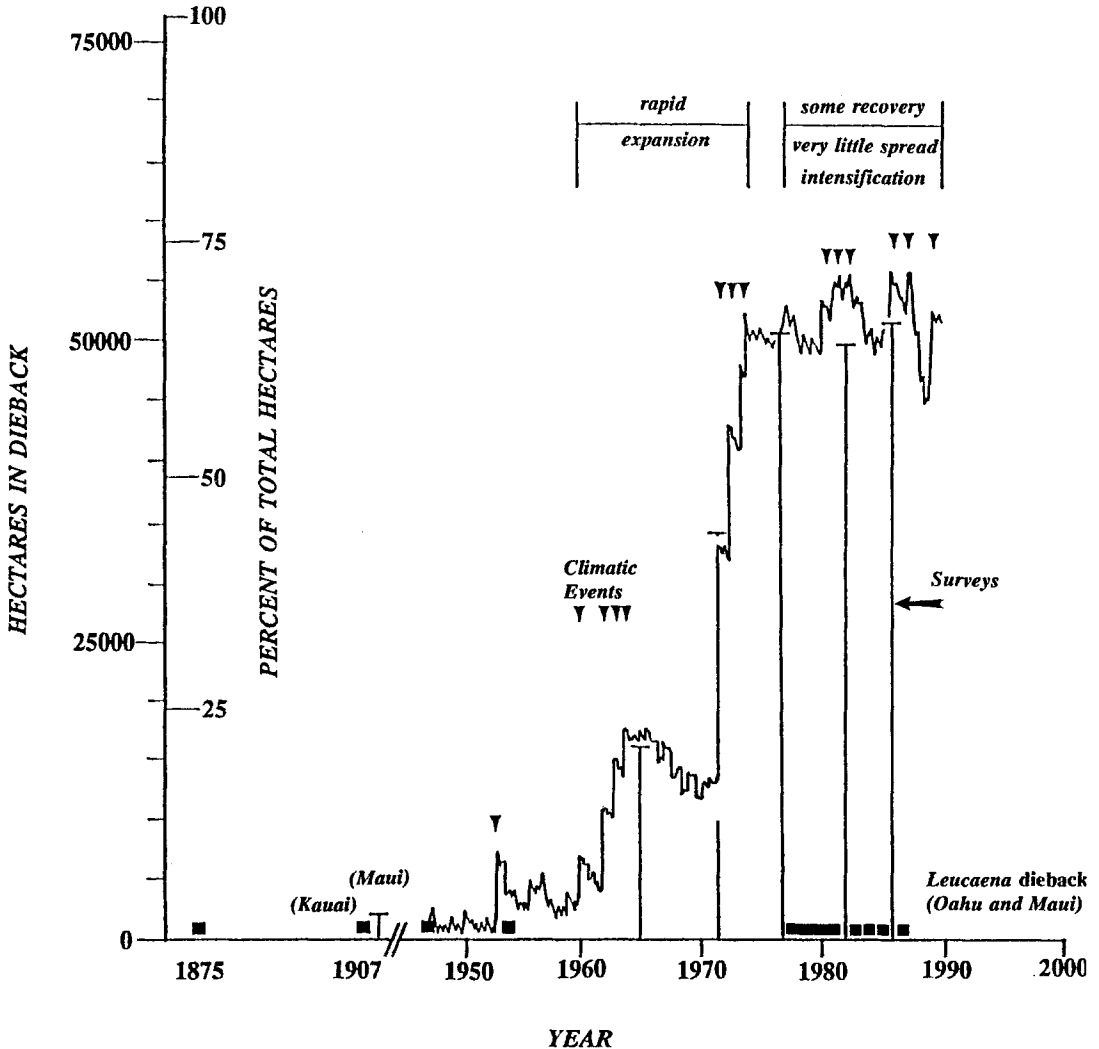


Fig. 2. Historical reconstruction of the forest crown diebacks in Hawaii, 1875–1990 based on a literature overview. Vertical bars show the areal extent of dieback on *Metrosideros* estimated from aerial and plot surveys. Arrows indicate rainless climatic events identified in Figure 3. See text for description of the dynamic trendline.

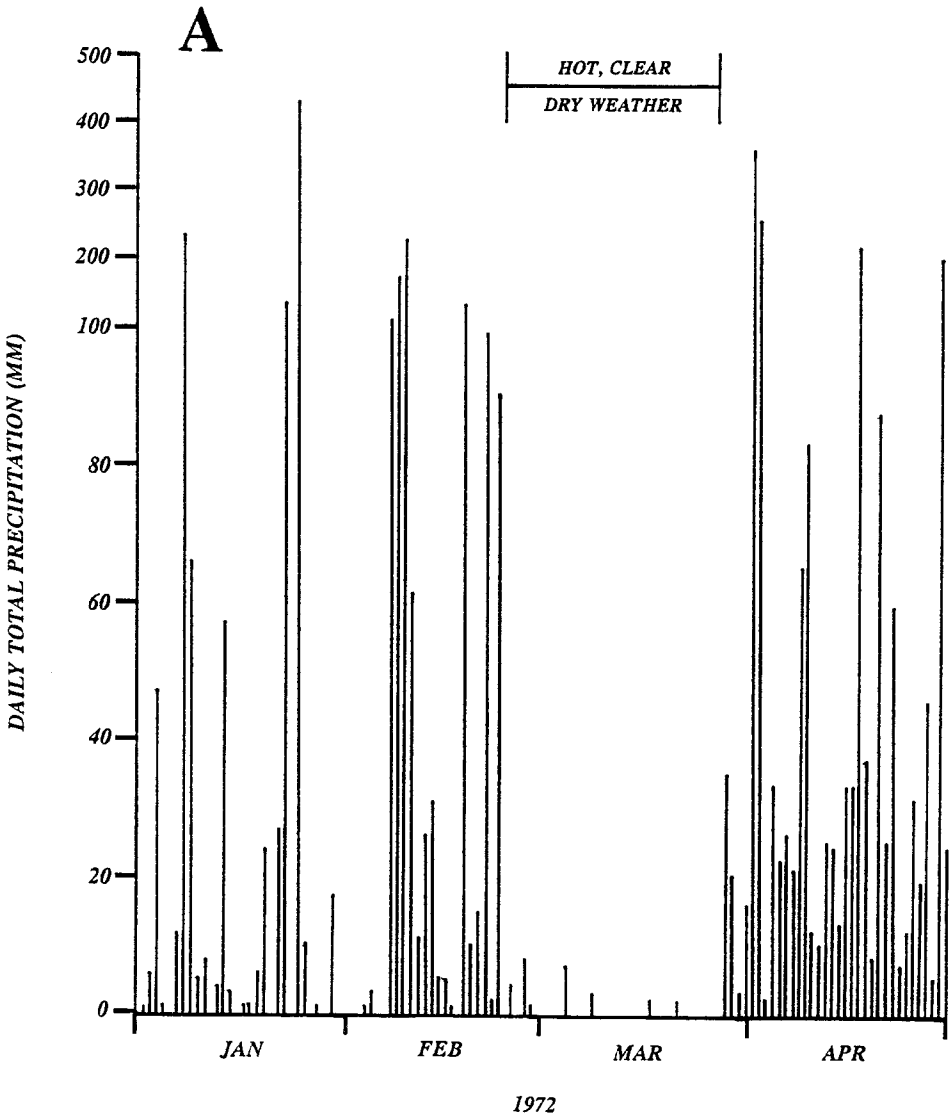
Researchers familiar with the dieback in the 1970's and early 1980's reported some recovery had occurred since the mid-1980's (Hodges *pers comm*, Kliejunas *pers comm*). This was probably due to a reduction of external stresses and an improved C balance following dieback of most of the crown (Jacobi *et al.*, 1988). Analysis of a 1990 re-survey of the 25 monitoring plots (above) was in progress (Jacobi *per comm*).

A significant feature evident in recent syntheses of the *Metrosideros* dieback was a dynamic pattern of initially localized patches; by the mid-1980's these had largely coalesced as a unit (Jacobi *et al.*, 1988).

It was also noteworthy that about 25% of the forest area has shown resistance over more than a decade of intensified dieback. The progression through expansionary, intensification and recovery phases was typical of some epidemic (biotic) diseases. In the intensely studied 1932-1958 dieback of birch (*Betula spp.*) in eastern Canada (Auclair *et al.*, 1992), recovery in birch was followed by continued dieback episodes in restricted locals.

The Rainless Event of March 1972

The similarity of the Hawaiian dieback to that on *Nothofagus* in New Zealand (Jane and Green, 1983) suggested that an appropriate focus would be on hot, clear



weather episodes. The marked rainy winter season from November through April (280 to 400 mm/mo) was associated with tradewinds from the northeast and frequently subject to heavy, low cloud cover (Burton and Mueller-Dombois, 1984). Hodges (*pers comm*) indicated that 30 days or more of clear weather would be highly anomalous over the main dieback area. A re-analysis of one such event, that of March 1972 (Evenson, 1983), indicated low or no rain over a 33 day interval (Figure 3a). This was accompanied by daily maximum air temperatures almost 3 °C warmer on average than adjacent intervals of wet weather (Figure 3b). Cloud

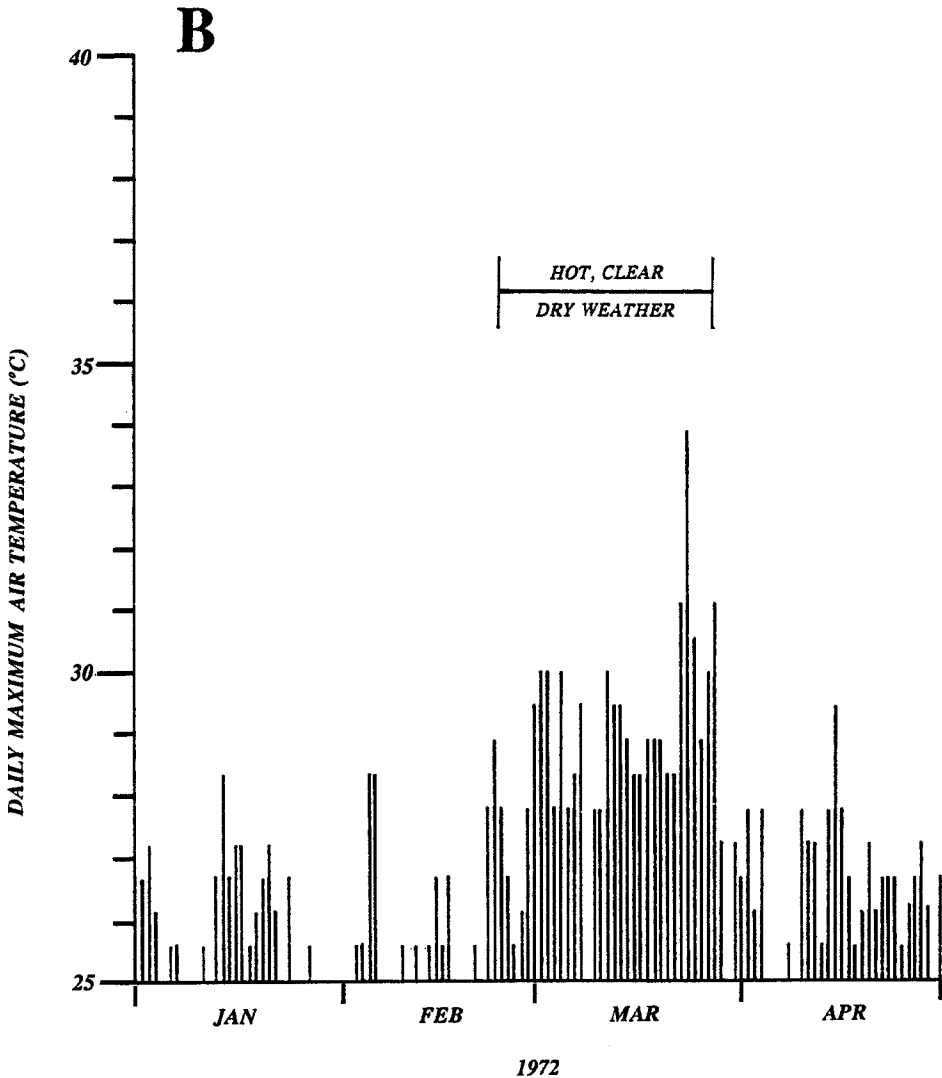


Fig. 3. Reconstruction of the rainless event of March 1972 based on daily meteorological records at Hilo, Hawaii (National Climatic Data Center 1990): (a) daily total precipitation, and (b) daily maximum air temperature, 1 January–30 April, 1972.

and sunshine data were available at Hilo but not analyzed in this study. The differences in maximum temperature, irradiance, and evapo-transpiration stress was expected to be much greater in the cloud zone than at Hilo.

In addition to very high levels of water stress during the hot rainless weather, the previous 30 days received five times more rainfall than normal in February; this increased the likelihood of sustained saturation of the soils on normally well-drained sites. The extremes of insolation when combined with reduced root growth

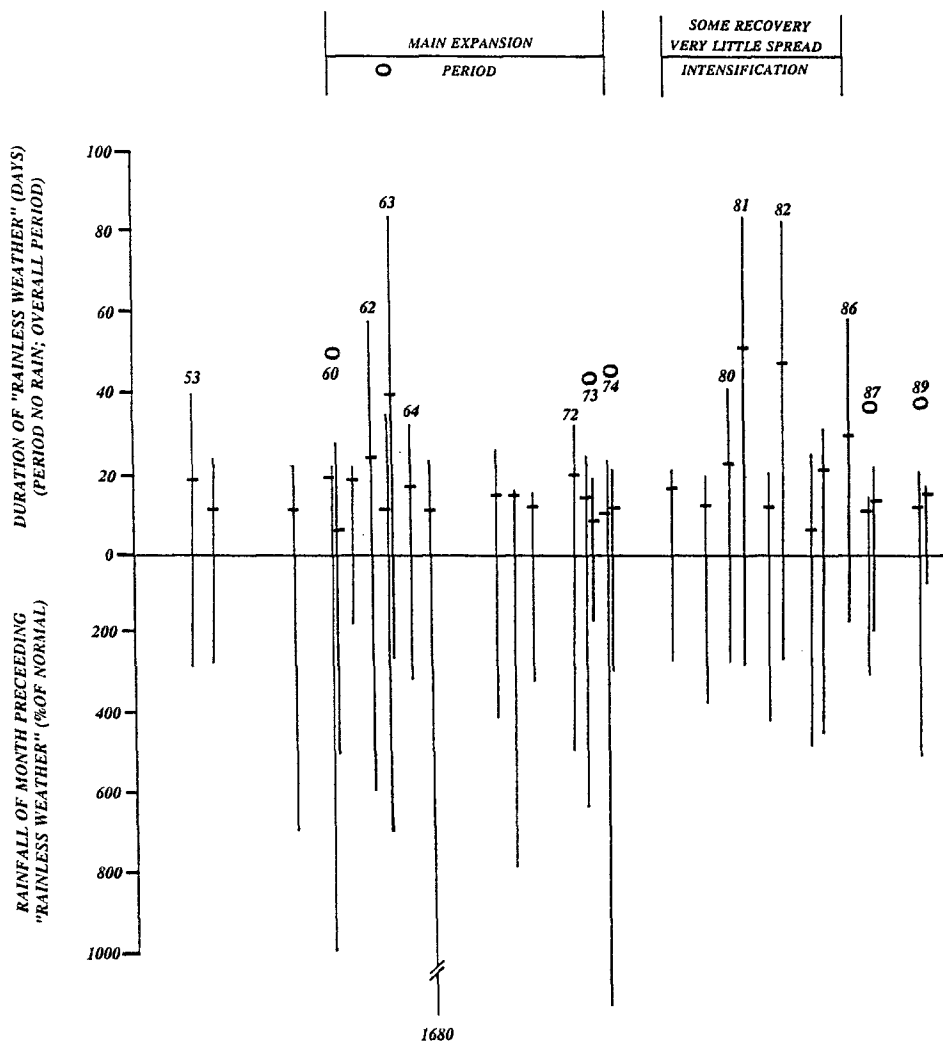


Fig. 4. Reconstruction of extreme wet/dry events potentially inciting cavitation injury on *Metrosideros* in Hawaii, 1950–1990 inclusive. Rainless weather events of 15 days of more duration have been identified by year in cases where the total duration [no rain (below bar) plus trace rainfall (above bar)] exceeded 30 days. Oval circles identify the combined duration of rainless weather in years with multiple events separated by two weeks or less. Bottom half shows the total rainfall of the 30 days preceding each rainless weather event. The main expansion and intensification periods of dieback are based on Jacobi (1983) and Jacobi *et al.* (1988).

on wet sites and/or flooding of well-drained soils were conducive to cavitation injury and I assumed this did occur.

Incidence of Rainless Events, 1950-1990

Episodes with 15 days or more of rainless weather occurred on 32 occasions over the 1950 to 1990 period (Figure 4). The pattern, however, was not random; four characteristic attributes were evident: (a) the rainless events occurred exclusively in the late fall and winter months, (b) the 11 severe episodes (30 days or more) tended to be clustered in the early 1960's, the early 1970's and through the 1980 decade. Episodes separated by two weeks or less, when summed, indicated that 1963 was particularly extreme as were 1981 and 1982. (c) There was good agreement between extreme episodes and the onset (1954), expansion (1960-1974) and the intensification (1980's) phases of the dieback on *Metrosideros*. (d) The rainless events in each case were preceded by heavy to extreme rainfall. Over the 30 days prior to each rainless event, rainfall averaged 4.6 times more than normal for the month in question. These several features substantiated the initial premise of an extreme climate-cavitation-dieback link.

Using the above evidence, it was possible to construct a trendline of *Metrosideros* dieback on Hawaii (Figure 2). To simulate the most likely changes in areal extent over time, the aerial and plot survey data were combined with the timing of the rainless events and with the author's knowledge of dieback etiology deduced from the pathology literature. A literature review indicated that forest crown dieback was episodic, with a definite abrupt onset, damage proportional to the climatic perturbation, and recovery in the absence of inciting stresses in at least a fraction of the population. The net result was a much more fluid or dynamic 'picture' of the dieback than has been perceived or described to date. The existing 'model' suggested that the fate of remaining healthy *Metrosideros* stands and the recovery of those already affected will depend on the balance between the recurrence of extreme climate and lapses of normal weather.

GENERAL DISCUSSION

The Approach

The strategy of scoping broadly and focusing on detail through a series of case studies was well-suited to the problems of dieback in the Pacific Rim. Not only were the forest types, climates, and dieback etiologies diverse, there were notable differences in methods, perception, and concerns among regions and researchers. There was a strong need for a synthesis and common framework capable of bridging the disparities and putting details of region-specific characteristics in perspective.

Conclusions

There was a high incidence of short-term extreme weather fluctuations capable of inciting irreversible cavitation damage on trees in most regions of dieback in

the Pacific Rim. It remained for well-designed field and laboratory experiments to demonstrate a link actually exists to dieback-affected trees; until actual evidence of cavitation disorders is available this link will remain conjectural. The dieback on *Metrosideros* in Hawaii since 1950 related closely to episodes of extreme rainfall followed immediately by clear, hot, dry, weather. The cause was not assumed to be drought *per se* but the combination of extreme wet-dry variation, as noted with studies of dying eucalypt in Australia (White, 1986).

Supporting Evidence

Was there sufficient factual evidence to justify a comprehensive project on a climate-cavitation-dieback mechanism? Five lines of experimental and observational data were relevant to this question.

First and foremost, massive cavitation injuries have been documented on trees with persistent crown dieback. Greenidge (1951) detected cavitation on dying yellow birch (*Betula alleghaniensis*) in New Brunswick, Canada and subsequently undertook a series of field and laboratory experiments to determine the inciting factors. A series of field treatments to induce extreme moisture stresses (eg excising of the root systems, varying degrees of cross-sectional incision through the trunk) were made on several tree species (Greenidge, 1954, 1955). These were only partly successful (Greenidge, 1990), probably because his focus was on summer drought rather than winter thaw-freeze as cause of the initial damage (Auclair *et al.*, 1992).

The presence of tyloses in the root xylem of jarrah in conditions associated with dieback in Western Australia (Wallace and Hatch, 1953; Davison and Tay, 1985) was also pertinent evidence. A variety of other early studies had identified dieback as a 'dysfunction of water transport' in affected trees without being able to specify a precise diagnosis (Podger, 1980; Pomerleau, 1991).

Second, the mysterious, unexplained nature of crown dieback symptoms was consistent with the invisibility of cavitation-type injuries. Greenidge (1951) had made numerous attempts through histological and microscopic examinations to detect blockages in the sapwood of dying birch and found no morphological abnormalities whatsoever; he had noted an excessive degree of 'vapor blocks', especially in branches of small diameter, but could not identify their origin. At the time of his studies, large questions remained to be resolved on the problem of the tensile strength of water (eg in closed tubes *versus* in plants) and theoretical studies of sap ascent and morphological structure were only beginning (Zimmermann, 1983).

Virtually all investigations of diebacks on Northern Hardwoods who had examined environmental stresses, focused on conditions in the growing season, that is, the summer period. The possibility of a winter injury that subsequently become evident only in the growth period had escaped notice. Exceptions were Braathe (1957) and Pomerleau (1991). The delayed expression of a cavitation injury added to its 'invisibility' in terms of diagnosing its origin; this feature of delayed expression may account for the focus on but poor resolution with respect to summer drought evident in many Pacific Rim and North American studies.

Recovery occurs and may be accounted for by the formation of new, functional xylem (and new root growth) in years subsequent to the injury. Processes of recovery, however, remained virtually unstudied. What fraction of the sapwood is actually involved in water conduction in tropical trees? In ring porous trees, is only the outermost annual ring relevant and if so is recovery more or less complete in one year? To what extent is new root tissue critical? Until key questions of this kind are addressed the mechanisms of persistence and recovery of dieback injuries will remain unresolved.

Studies in eastern North America suggested strongly that the dieback 'pathology' is a physiological dysfunction of the tree conductive system, namely a massive, irreversible cavitation injury to the sapwood that acts to limit or block the transport of water through vessels and tracheids (Greenidge, 1951; Auclair *et al.*, 1992). The primary factors inciting cavitation are moisture and/or freezing stresses (Tyree and Sperry, 1989) but the ecology and etiology (onset, progress, and recovery) are poorly understood and not quantified. Only in the past five years have systematic studies been done to determine the action of environmental factors in the origin and development of cavitation phenomena (Sperry and Tyree, 1988; Sperry *et al.*, 1988a,b,c; Tyree and Sperry, 1988, 1989). This new information has yet to be applied to practical problems such as orchard, nursery and plantation mortality and dieback in natural tree populations.

Third a central observation in the *Metrosideros* and other forest diebacks was the relatively great severity of crown dieback in mature cohorts of the population. The term 'cohort senescence' had been closely associated with the problem and several theories have been proposed to explain the phenomenon (Mueller-Dombois, 1983; Gerrish, 1988, 1990). Cavitation theory appeared to offer a straightforward explanation since there was an exponentially increased risk to cavitation with increasing age. This was based on the increased length of tracheids in stemwood of mature trees, the probability of cavitation increasing as a square of element diameter or length (Zimmermann, 1983).

Fourth, there was remarkable similarity in the dieback symptoms reported among the differing regions, episodes and species affected. Podger (1980) had noted this feature and suggested that a common mechanism may underlie these diebacks. Cavitation directly affects the variability and health of the crown and one would expect that as an aggregate, the symptoms would be highly consistent with a process of water blockage irrespective of the environmental milieu or species idiosyncracies.

Fifth, it is now widely recognized that crown dieback is not a disease but a disorder internal to the plant. As an injury, irreversible cavitation is intimately related to external stress, both in its origin (extreme climatic fluctuations) and in rendering the tree hypersensitive to moisture stresses subsequent to the injury.

Research Directions

There was a need for investigating the presence of dysfunctional cavitation in trees using the most recent technologies. Accurate information on cavitation in dieback-

EXTREME CLIMATIC FLUCTUATION

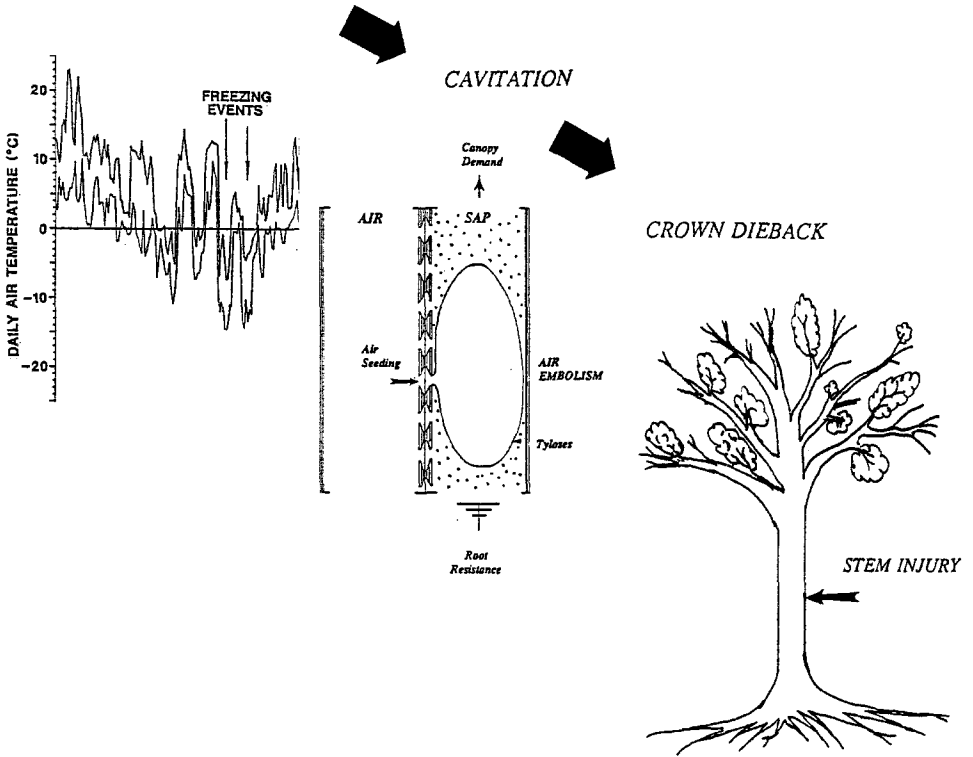


Fig. 5. Schematic illustration of the extreme climate-cavitation-dieback link proposed as a future research focus.

affected trees was virtually absent but crucial to testing the conclusions of this paper.

A variety of authors have experimentally induced crown dieback by manipulating snow cover in winter months (Pomerleau, 1991; Robitaille, 1991), and in acute frost desiccation (Pomerleau, 1991; Swanson, 1983) and summer drought (Greenidge,

Conceptual Model for Inter-regional Comparisons

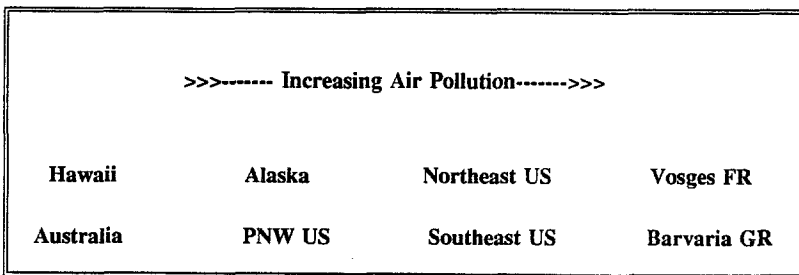


Fig. 6. Conceptual framework for an inter-regional, multi-national research study designed to address the problem of primary stresses inciting forest crown dieback.

1954; McMinn, 1956; Pomerleau, 1991; Robitaille, 1991) treatments. Some of these experiments need to be re-examined and re-designed to include simultaneous measurements of tissue water stress and *in situ* cavitation responses (Figure 5).

There was a strong need for comparative approaches both within regions and across the broad spectrum of contrasting regions globally. Sinclair (1965) had elucidated the fundamental principals of forest dieback and decline etiology by inter-comparing three major diebacks in the Northern Hardwoods. An inter-regional, multinational project based on a comparison of dieback responses to climatic stress promises to yield much new insight into the forces inciting and exacerbating dieback (Figure 6). It would also serve to integrate much of the current observational and experimental evidence on the problem, and factor out the effects of regional air pollution (eg O₃, heavy metals, acidic deposition) from natural stresses (ie climate, insects and diseases, cohort senescence). Until such a disaggregation is achieved, the management of dieback problems will remain uncertain.

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