DAVE KELLY and MEGAN R. OGLE

Plant and Microbial Sciences, University of Canterbury, Christchurch 1.

A TEST OF THE CLIMATE HYPOTHESIS FOR DIVARICATE PLANTS

Summary: To test the hypothesis that the divaricate habit protects internal leaves from cold and dry conditions, and raises leaf temperatures on cold sunny days, thermocouples were attached to internal and external leaves on divaricate plants. For *Coprosma propinqua* plants at Cass, inland Canterbury, there were consistent differences in temperature between leaves, but these were not simply related to their canopy position (interval vs. external). While leaf temperatures fell as low as - 9.5 °C on frosty nights, internal leaves were not consistently warmer (between 0.28 °C warmer and 0.04 °C colder) than external leaves. Consistent differences in temperature between leaves were not clearly related to their position or degree of exposure. Internal leaves near the top of the canopy were often close in temperature to external leaves at the same height. Specific humidity was higher inside the bush than outside, but again the effect was small. On calm, sunny winter days, internal leaves were usually slightly cooler than external leaves. For *Hoheria angustifolia* on the Port Hills, there was only a slight temperature difference between internal and external leaves (0.3 to 0.5 °C). Overall, the temperature and humidity data give little support to the climate hypothesis. However, there was more damage (apparently due to frost) to *Coprosma propinqua* leaves on the outside of bushes over winter 1989, suggesting that the biological significance of the divaricate habit may be greater than these physical data would indicate.

Keywords: Divaricate shrubs; divaricating; climate hypothesis; moa browsing; *Coprosma propinqua; Hoheria angustifolia;* leaf temperature; relative humidity.

Introduction

Some parts of New Zealand are remarkable for the large number of similar-looking shrubs which have small leaves and tangled, interlaced branches. These are called divaricate (Cockayne, 1912). Characteristic features include much-branched, wiry stems; wide branching angles, often almost at 90°, producing an interlaced structure; the development of many short shoots; small entire leaves concentrated in the interior of the plant; and lateral flowering (Cockayne, 1912; Bulmer, 1958; Greenwood and Atkinson, 1977; Tomlinson, 1978; McGlone and Webb, 1981; Atkinson and Greenwood, 1989). Also, divaricating plants in New Zealand typically lack spines.

A large fraction of the native flora (10070 of all woody species) has the divaricate habit (Greenwood and Atkinson, 1977), including both shrubs which remain permanently divaricate, and trees which have a divaricate juvenile form. This percentage is claimed to be higher than in many other parts of the world (Dawson, 1988). However, other areas such as California and Arizona have many divaricate plants, similar to those in New Zealand except for the presence of spines (Tucker, 1974). The same may be true of Argentina. Therefore, it is not clear whether the remarkable feature of the New Zealand flora is the high percentage of divaricates, or the high percentage of divaricates which lack spines. This is really a debate about the definition of a 'divaricate'.

Regardless of the relative frequency of divaricates in New Zealand and overseas, the habit has arisen here in so many different genera, and is so prevalent in some communities (Greenwood and Atkinson, 1977), that it has prompted debate on the possible evolutionary advantages of being divaricate. Two main theories have been advanced: that it is an adaptation to climate (Diels, 1897; Cockayne, 1912; McGlone and Webb, 1981); or that it is a response to moa browsing (Greenwood and Atkinson, 1977; Atkinson and Greenwood, 1989).

The moa browsing hypothesis has been very successful in prompting further study and debate on this topic. In its favour is that the moas were unique to New Zealand, which makes it easier to explain any unique frequency of divaricates or lack of spines in the local vegetation. The hypothesis, perhaps unfairly, became less popular as a result of the discovery of subfossil moa gizzards containing twigs from a number of divaricate plants (Burrows, 1980; Burrows, McCulloch and Trotter, 1981; Burrows, 1989). The gizzard samples prove that mos did eat divaricate plants, and were capable of shearing off entire twigs. This evidence alone does not exclude moa browsing as a selective force favouring the divaricate habit. What would be needed are data on the relative abundance of the plants in the vegetation and the diet, in order to calculate preference ratios for the various plants (divaricate and non-divaricate) eaten by moas. Unfortunately, as the animals are extinct such calculations cannot be done, and the moa hypothesis cannot be rigorously tested in this manner.

The climate hypothesis is, in contrast, eminently testable. The basic theory is that the growth form is an adaptation to an inhospitable climate which was dry (Diels, 1897), windy (Cockayne, 1912) and frosty (McGlone and Webb, 1981), either recently or during the Pleistocene glaciations. In the most recent exposition of this hypothesis, McGlone and Webb (1981) suggested that the tangled branches serve as a windbreak and frost screen. This leads to three explicit predictions: (1) that leaves in the interior of the plant may be partly protected from the effects of frosts; (2) the branches may serve as a heat trap on sunny winter days, raising the temperature (and thus the photosynthetic rate) of interior leaves; and (3) the interior of the plant may be more humid, reducing water loss.

Tests of the climate hypothesis might be conducted in several ways. Firstly, physical variables like leaf temperature, relative humidity, and wind speed can be directly measured inside and outside the canopy of divaricate plants, in order to estimate the magnitude of any amelioration in microclimate within the plant. Secondly, inside leaves may be effectively relocated to the outside of the plant, by chopping off the top to leave them exposed. These newly-exposed leaves may be examined for any different in responses (e.g. incidence of frost damage) from internal leaves which remain protected. This is using the leaves of the plant itself to-measure the microclimate, which may be the most appropriate way of determining whether any amelioration of climate is significant. Thirdly, in heteroblastic species with divaricate juvenile forms, mature leaves may be tied down to bring them as close to the ground as juvenile leaves on the same or nearby plants. Again, differences in actual leaf temperature or leaf responses to climate may be recorded.

The aim of this study was to test the climate hypothesis, both by direct measurement of the physical environment inside and outside divaricate plants, and by manipulating the position of leaves to use them as biologically relevant 'climate sensors'. In particular, the following questions were addressed:

(1) Are internal leaves warmer, on average, than external leaves during frosty conditions?
(2) Are internal leaves warmer, on average, than external leaves during calm, sunny days in winter?
(3) Is there any measurable difference in humidity inside and outside a divaricate plant?
(4) Are external leaves more liable to frost damage than internal leaves, and are internal leaves more liable to frost damage when the protecting lattice of branches above them is removed?
(5) Are mature leaves of heteroblastic species colder than juvenile leaves at the same height?

Methods

Climate measurements were made using Campbell CR21X dataloggers, on two different plant species: a divaricate shrub, *Coprosma propinqua,* and a heteroblastic tree with a divaricate juvenile form, *Hoheria angustifolia*. Nomenclature follows Allan (1961).

Climate recording equipment

Three dataloggers were used to measure leaf temperature, air temperature, and air relative humidity. Each datalogger can record 16 different sensors. Leaf temperatures were measured using small copper-constantan thermocouples (wire 0.25 mm diameter, junction length 4 mm) which were tied to the petioles with thread, and fastened to the underside of leaves with a small quantity of thermal paste (Red point Thermapath 167, available at electronics suppliers). The thermal paste kept the thermocouples in contact with the lower leaf surface, and caused no visible damage to the leaves. A calibration experiment in Christchurch using thermocouples attached to leaves with and without thermal paste, showed that the thermal paste did increase the thermal lag of the leaf-thermocouple unit, but this was only significant while temperatures were changing rapidly (such as when the sun came out after a frost). In extremely frosty weather, the paste sometimes hardened, causing the paste and thermocouple to detach from the leaf. However, the calibration experiment indicated that the thermocouple coming away from the leaf did not cause a large change in the recorded temperature, as long as the thermocouple was close to the underside of the leaf and there was no direct solar radiation.

Air temperature was recorded using thermocouples inside small perforated radiation shields. Relative humidity was recorded using Campbell 207 probes, which incorporate a thermistor and a ceramic humidity-sensitive chip; the probes are 11 cm long and 3 cm diameter.

The dataloggers were programmed to sample each sensor every 60 seconds. Every hour, averages of all 60 readings on each sensor were stored for later use. Daily averages, standard deviations and minima for each thermocouple were recorded daily at 9 a.m. In addition, when the temperature of any themocouple fell below 0°C, average temperatures for all themocouples were stored every 10 minutes.

The dataloggers measure the sensors with an error of ±0.1 %. The thermocouples were calibrated together at the end of the experiment, at which time they were all within ±0.21°C, and mostly within 0.05°C; the appropriate correction factor for each thermocouple was subtracted from the stored data if the error was more than 0.05°C. The largest potential source of measurement error was the use of the panel temperature of the CR21X as a reference temperature for all the thermocouples. When the temperature of the CR21X is changing rapidly, this may give an error of ±0.2°C (Campbell Scientific, 1986). Since the data of most interest here were obtained at night with relatively stable temperatures in the range of 0 to -10°C, the typical error is probably smaller than 0.10°C.

Coprosma propinqua at Cass

Coprosma propinqua was studied at Cass (43 ° 02' S, 171 ° 45' E), in inland Canterbury 22 km east of the main divide of the Southern Alps. This area was chosen because the open, grassy basins of the braided high country rivers are the kind of exposed, frosty environment mentioned by McGlone and Webb (1981) as likely to favour the divaricate habit.

The study site was at 680 m altitude on an alluvial fan (slope 10°, aspect 240°) behind the University of Canterbury field station. Vegetation on the fan was scattered bushes of *Coprosma* and *Discaria toumatou* over a short-tussock grassland dominated by *Festuca novae-zelandiae, Poa colensoi,* and *Agrostis capillaris*. The area was covered in *Nothofagus solandri* var *cliffortioides* forest until a series of fires about 500 years ago killed the trees (Burrows, 1977).

Humidity and leaf temperatures

Two groups of *Coprosma* plants, 75 m apart, were used. At the first, the 'chopped' site, 15 leaves were studied at a constant height of 90 cm ±5 cm from the ground on three *Coprosma* plants. One of the three plants was naturally just over 90 cm tall, and the other two were trimmed to that height. Three types of leaves were recognized: 'internal' (shielded by branches), 'external' (leaves on the edge or top of the bush, open to the sky), and 'newly exposed' (previously-internal leaves which were rendered external by trimming the bush). Thermocouples were attached to six internal, five external, and four newly-exposed leaves.

At the second site, the 'RH' site, pairs of internal and external leaves were studied at heights of 40, 95, 125 and 165 cm from the ground on a single *Coprosma* bush, giving eight leaves in all. Additionally, air temperature and relative humidity were recorded inside and outside the bush at heights of 115 cm (temperature) and 90 cm (RH).

The dataloggers were run from 7 May to 26 June 1989.

Leaf damage in the field

Healthy leaves were marked on 30 April with small spots of red nail polish to study the amount of frost damage, defined as brown or black tissue damage on the leaves. There was no evidence that the nail polish was causing any damage to leaves. In total, 50 internal, 40 external and 20 newly-exposed leaves were marked in the RH and chopped stands. Leaves were relocated and assessed for damage on 21 July 1989.

Wind and sunshine data

Readings from an automatic weather station at the Geography field station in Chilton Valley, 2 km east of the study site, were used for wind and sunshine data, and for air temperature readings from 1985 to 1989.

Hoheria angustifolia on the Port Hills

This tree has divaricate juvenile growth form, changing to an erect, less-branched, large-leaved form at a height of about 2 m. It was studied at the head of Hoon Hay Valley (43 o 37' S, 172 o 38' E) on the Port Hills near Christchurch. The site was at an altitude of 450 m. A stand of about 12 small *Hoheria* trees surrounded by pasture was used. One of the trees was tied down so that mature foliage, previously at a height of 250 cm, was held at a height of 95 cm. Using thermcouples, temperatures were recorded for three juvenile internal leaves, three juvenile exposed leaves, and three mature exposed leaves at a height of 95 cm; and for three mature exposed leaves at a height of 250 cm. Air temperatures at 95 and 250 cm were also recorded. Data were recorded for the period from 17 June 1989 to 27 July. A series of heavy frosts in the period 22 July to 27 July provided the coldest temperatures over that time, so only those data are presented.

Leaves were not marked with nail polish for *Hoheria,* because it is semi-deciduous, and many leaves are shed over the winter.

Analysis

Frost events were defined as periods when any thermocouple was below 0°C for more than hour; if two frosts were separated by less than one hour above zero, they were treated as a single frost. Over the duration of each frost, mean temperatures for internal and external leaves at a site were calculated; these were compared over the whole study period using paired t-tests.

To search for a 'heat trap' effect in *Coprosma propinqua* on calm, sunny winter days, hourly data were included if the average solar radiation exceeded 100 watts m^{-2} and the average wind speed was less than 2 m sec^{-1} (both measured in the Chilton Valley).

The standard deviation of the temperature of each leaf was recorded daily. These were tested by dividing the internal mean standard deviation by the external mean standard deviation, and taking the log of the result. These were then tested with a sign test.

The relative humidity data were converted to specific humidities (in grams of water per kg of moist air) in order to remove the temperature dependence shown by relative humidities (Oke, 1978).

Results

Coprosma propinqua at Cass

Weather over the study period

In early May and late June there were spells of warm, sunny days, while early June brought several snowfalls. There were frosts in both months. Mean daily air maximum and minimum temperatures from the Chilton Valley were similar in May 1989 (9.8 and 2.2∞∞C) to the average for 1985-88 (10.2 and 2.1∞∞C), but June 1989 was 1∞∞C colder (5.9 and -0.7∞∞C than 1985-88 (6.7 and 0.6∞∞C).

At the *Coprosma* plants, air temperature ranged between -9.5 and 19∞∞C over the study period.

Mean leaf temperatures during frosts

Between 9 May and 26 June there were 19 discrete frost events, ranging from just under five hours, to over 24 hours long (Table 1). Mean wind speeds during the frosts ranged from 0.7 to 4.5 m sec^{-1}. Leaf temperatures were below freezing for 23% of the study period (Table 1), including 16% of daylight hours and even 9% of the time in direct sunlight (while ice thawed). The lowest leaf temperature recorded was - 9.5∞∞C for external leaves at both sites.

Mean temperatures over each frost for all internal and external leaves at each site are given in Table 1. At the RH site, internal leaves were consistently warmer than external leaves by a small amount in all of the 19 frosts. The difference, which averaged 0.28 ∞∞C, was significant (paired t-test, t = 10.2, d.f= 18, $p<0.001$). However, at the chopped site,

Table 1: *Frosts recorded between* 7 *May and* 25 *June* 1989 *at two groups of* Coprosma propinqua *plants at Cass, inland Canterbury. The length of the frosts,* minimum *leaf temperatures, mean internal and external leaf temperatures for the duration of the frost (recorded* every *60 seconds), and* wind speed *data from the Chilton Valley,* 2 *km away, are given. All values are in degrees Celsius* unless *specified.*

Date	RH site Length (Hr:min)	Min Temp	Mean Int	Mean Ext	Chopped site Length (Hr:min)	Min Temp	Mean Int	Mean Ext	Chilton Valley Wind (m sec^{-1})
May 9	12:20	-4.0	-1.97	-2.29	12:10	-5.1	-2.97	-2.93	2.6
May 10	12:20	-5.6	-2.59	-2.92	12:10	-6.4	-3.75	-3.68	0.7
May 11	8.20	-2.0	-0.10	-0.56	9:00	-2.7	-1.33	-1.25	1.4
May 19	8.20	-2.1	-0.29	-0.65	11:20	-2.8	-1.27	-1.20	1.4
May 26	5:10	-1.4	0.15	-0.19	4:50	-2.0	-0.68	-0.58	2.1
May 28	11:10	-5.2	-2.39	-2.84	11:40	-6.0	-3.66	-3.57	2.1
May 29	11:40	-1.7	-0:67	-0.73	24:50	-2.8	-0.86	-0.74	4.5
May 30	21:10	-1.8	-0.64	-0.77	5:50	-2.8	-0.77	-0.80	3.8
May 31	21:00	-9.5	-4.48	-4.77	20:40	-9.5	-4.77	-4.79	0.7
June 1	14:10	-7.7	-4.21	-4.73	14:40	-8.7	-5.37	-5.37	1.0
June 4	20:20	-5.0	-2.05	-2.25	19:00	-5.9	-2.77	-2.72	1.7
June 5	20:50	-6.6	-2.24	-2.40	20:40	-7.3	-2.80	-2.79	0.8
June 6	19:10	-6.4	-3.08	-3.32	19:40	-7.0	-3.55	-3.59	1.2
June 13	8:30	-1.4	-0.32	-0.64	9:40	-2.3	-1.02	-1.03	2.1
June 16	9:40	-1.3	0.12	-0.05	4:50	-1.6	-0.21	-0.21	2.3
June 17	18:20	-6.7	-3.37	-3.70	19:00	-7.8	-4.03	-4.05	1.1
June 21	14:40	-4.2	-1.80	-2.01	15:50	-4.2	-2.13	-2.08	2.0
June 23	17:20	-4.5	-1.59	-1.79	17:20	-4.9	-2.12	-2.11	0.9
June 24	14:10	-3.0	-0.89	-1.11	14:20	-5.3	-1.63	-1.61	1.0
MEAN			-1.71	-1.99			-2.41	-2.37	

mean internal and external leaf temperatures were almost exactly the same (the difference in means was 0.04∞C. In 17 of the 19 frosts, the means differed by less than 0.1∞C.

At the chopped site, newly-exposed leaves were colder than external leaves at the same height by 0.20∞C (averaged over all 19 frosts).

There was a close relationship between wind speed during each frost, and minimum leaf temperatures at both the RH and chopped sites (r = 0.689 and 0.688 respectively, wind log-transformed, n = 19, p<0.001 for both). At the RH site only, the difference between mean internal and external temperatures during each frost showed a weak non-linear relationship to wind speed (only small differences were found at high wind speeds, but a range of differences at low wind speeds; Table 1). However, there was no significant relationship at either site between the size of the temperature difference and minimum leaf temperatures (r = - 0.24 and -0.40 at the RH and chopped sites respectively; N.S.).

The time-course of the temperature difference between internal and external leaves is shown for the week ending 6th June, which included the coldest frosts over the study period. Hourly mean internal

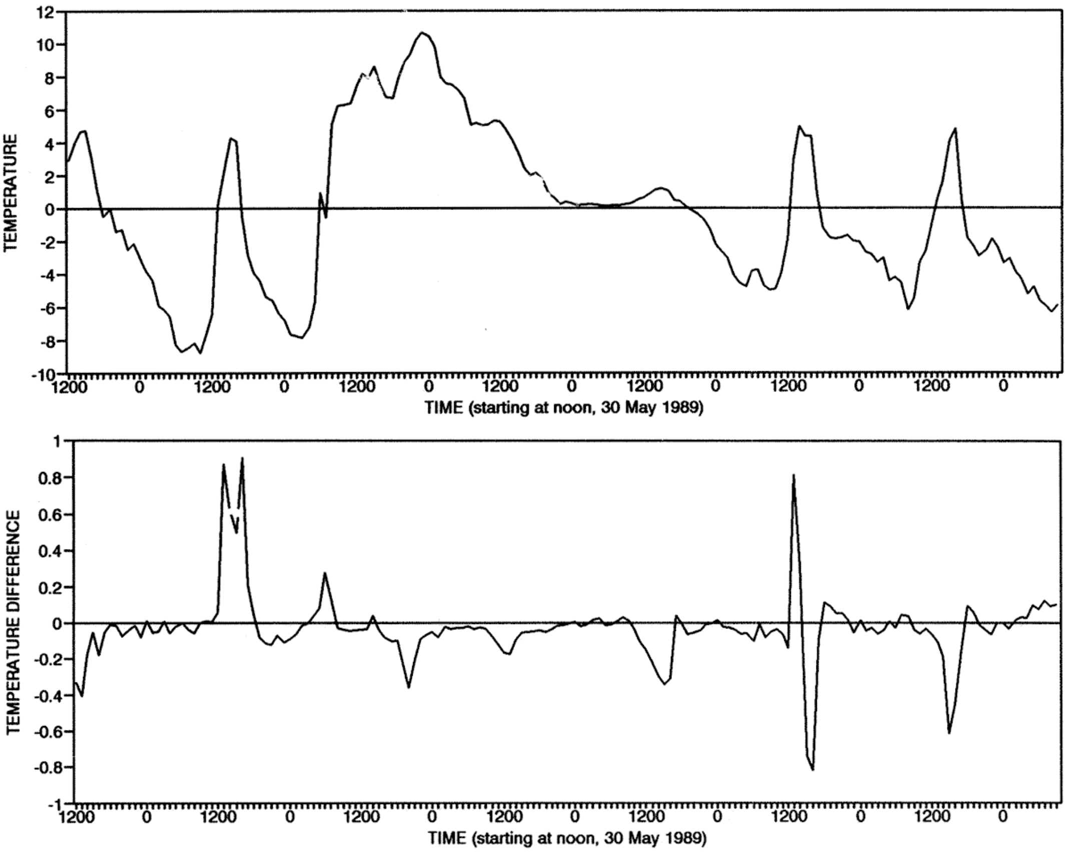

Figure 1: *Hourly mean leaf temperatures for* Coprosma propinqua *at the chopped site, Cass, inland Canterbury, sampled every 60 seconds from 30 May to* 6 *June* 1989. *(a) Temperatures of external leaves (five replicates). (b) Difference between internal (six replicates) and external leaves. A positive difference means the internal leaves were warmer.*

leaf temperatures were colder than external leaves for nearly the whole time (Fig. 1b), except for brief periods when the leaves were warming up rapidly (Fig. 1a gives the absolute temperatures of the external leaves).

The same pattern was shown by the 10 minute averages recorded during each individual frost. For example, during the coldest frost (May 31, leaf temperatures down to - 9.5∞C) internal leaves were rarely warmer than external leaves at the chopped site (Fig. 2).

Individual leaf temperatures during frosts

The temperatures of individual leaves were examined for the chopped site, where there was little difference between mean internal and external leaf temperatures. Within anyone frost, both internal and external leaves showed a wide spread in mean temperatures over a similar range (Fig. 3). The pattern of relative temperature was constant over all the coldest frosts: for the two coldest (shown in Fig. 3), the Pearson correlation coefficient was 0.814 ($p<0.001$). For all 14 other pairwise comparisons of individual leaf

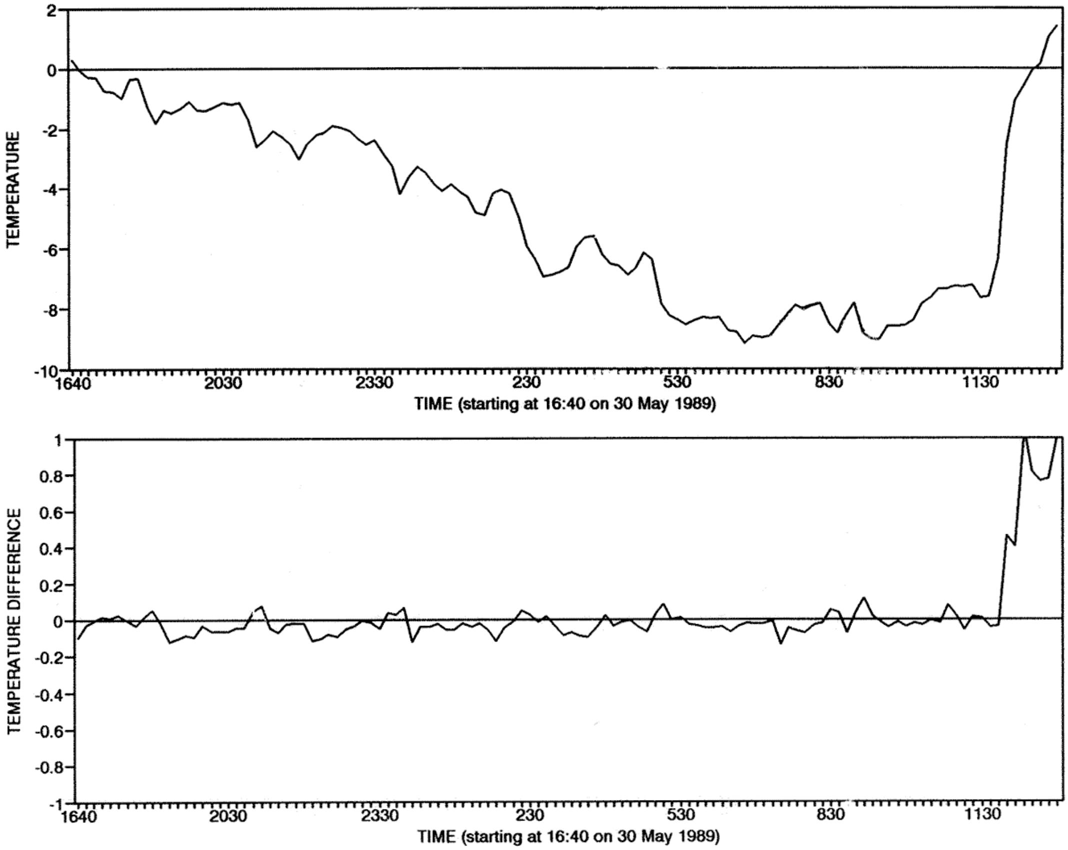

Figure 2: *Ten-minute means of leaf temperature for* Coprosma propinqua *at the chopped site. Cass, inland Canterbury, sampled every 60 seconds during a heavy frost on 30-31 May* 1989. *(a) Temperatures of external leaves (five replicates). (b) Difference between internal (six replicates) and external leaves. A positive difference means the internal leaves were warmer.*

temperatures in the six coldest .frosts, the temperatures were highly correlated (r = 0.623 to 0.957; p = 0.012 in one case and <0.001 for the rest).

Therefore, at the chopped site, there were consistent small differences in leaf temperature, but these were not related to the internal or external location of the leaf.

Variation in leaf temperature

The standard deviation of the individual leaf temperatures varied widely from day to day, from 0.03 to 2.30. However, the internal leaves had smaller mean standard deviations than external leaves on the same day in 43 of the 49 cases. This was highly significant (sign test, p<0.001).

Leaf temperatures on sunny days

Periods of bright sunshine and low wind speeds, which might provide the ideal conditions for a heat trap effect to operate, occurred on thirteen days (Table 2). Over most of these periods, external leaves were warmer than internal leaves at both the chopped and RH sites. At the chopped site, the three periods when internal leaves were warmer all occurred on days with high solar radiation input. However, this was not true of the RH site. Overall, the average temperatures seem to contradict the hypothesis that a heat trap effect was raising the temperatures of internal leaves, even on calm, sunny days.

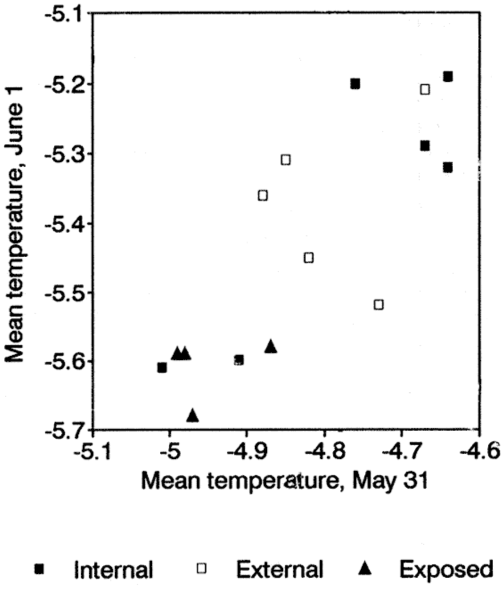

Figure 3: *Mean temperatures of individual leaves of* Coprosma propinqua *at the chopped site, Cass, inland Canterbury, over the duration of the two coldest frosts during the study period (30-31 May and* 31 *May-1 June).*

Table 2: *Calm, sunny periods recorded between* 7 *May and* 26 *June* 1989 *at two groups of* Coprosma propinqua *plants at Cass, inland Canterbury. The length of the interval, mean solar radiation, mean wind speed (both from Chilton Valley), and mean internal and external leaf temperatures (recorded every 60 seconds) are given for the duration of the period. All values are in degrees Celsius unless specified. Values marked* indicate an internal temperature greater than its corresponding external pair.*

		Chilton Valley		RH site		Chopped site	
Date	Duration (hr)	Radiation (W m^{-2})	Wind (m sec^{-1})	Mean Int	Mean Ext	Mean Int	Mean Ext
May 9	5	227	0.5	3.75	4.45	4.92	4.94
May 10	5	215	0.4	5.03	5.61	6.02*	5.92
May 18	4	342	0.5	6.58	7.32	9.11*	8.79
May 25	5	155	0.5	8.04	8.32	8.50	8.61
May 30	2	216	1.1	2.89	3.42	4.01	4.30
May 31	3	251	0.3	-4.29	-4.23	-0.89*	-1.40
June 9	4	152	1.2	6.09	6.19	6.41	6.43
June 19	5	157	1.4	4.36	4.51	5.04	5.33
June 20	2	145	1.5	4.96	5.07	6.16	6.44
June 21	4	114	0.6	4.59	4.79	5.18	5.28
June 23	2	140	1.8	2.94*	2.89	4.08	4.19
June 24	3	112	0.1	2.06	2.13	2.31	2.41
June 26	5	140	0.9	4.23	4.38	4.74	4.93
MEAN				3.94	4.22	5.05	5.09

Humidity

The specific humidity inside the RH plant was usually higher by 0.2-0.4 g kg^{-1}), while the absolute levels external to the bush ranged from 2 to 7.5 g kg^{-1}. (Fig. 4).

Table 3: *Leaf damage (presumably due to frosts) on marked internal, external, and newly-exposed leaves on* Coprosma propinqua *plants at Cass between 30 April and* 21 *July* 1989. *Data are number of leaves except where stated.*

Position	Marked	Relocated	Damaged	% damaged
Internal	40	33	0	0
External	50	35	11	33
Exposed	20	16	12	75

Leaf damage

There was more damage to external and exposed leaves than to internal leaves on the *Coprosma* plants during this study (Table 3). The difference was significant (chi-square = 12.37, d.f. = 1, $p<0.001$). More newly-exposed leaves than external leaves were damaged (chi-squared = 8.42; d.f. = 1, $p<0.001$).

Hoheria angustifolia on the Port Hills

Weather over the study period

The Port Hills site experienced unusually calm, frosty weather in late July. Daytime air temperatures ranged from 10 to 14∞C, while night temperatures fell as low as - 3.3∞C.

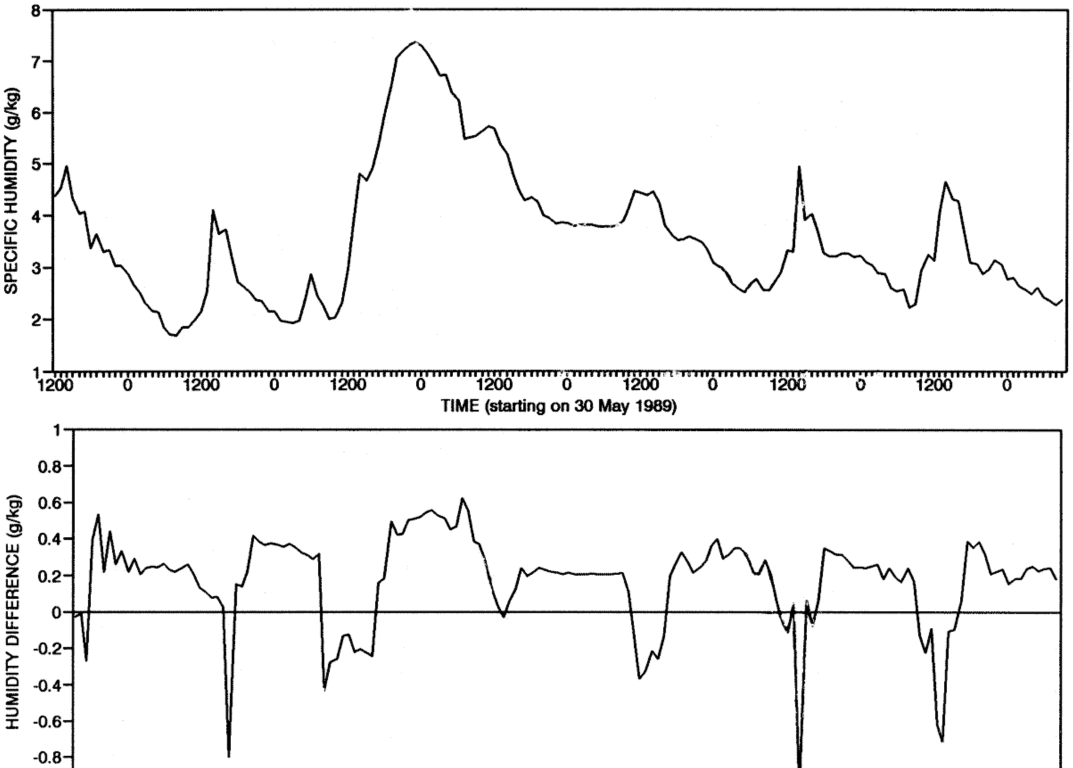

Figure 4: *Hourly mean specific humidity inside and outside a* Coprosma propinqua *bush at the RH site, Cass, inland Canterbury, sampled every 60 seconds from 30 May to* 6 *June 1989. (a) Specific humidity* (g H_2O kg^{-1} *moist air) external to the bush. (b) Difference between internal and external humidity. A positive difference means the internal air was wetter.*

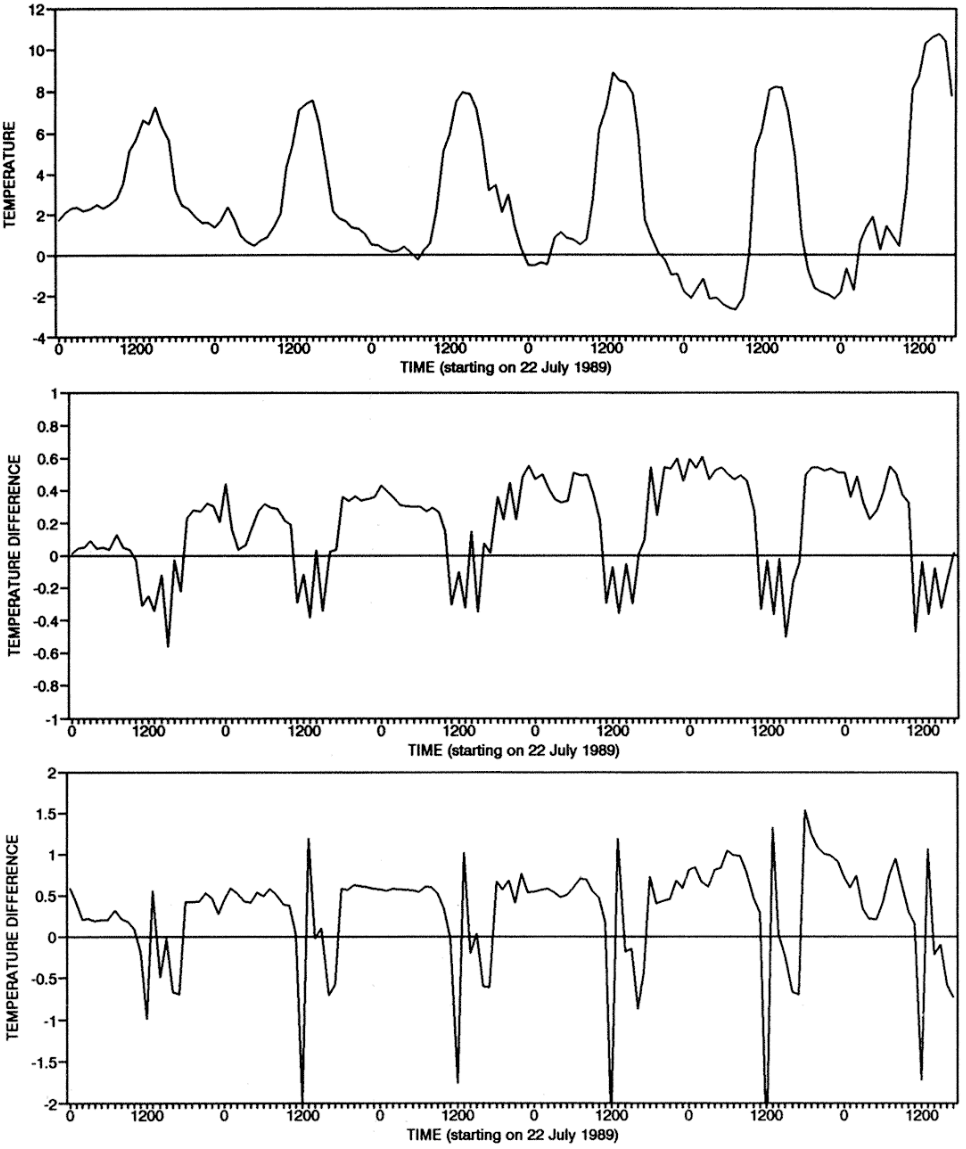

Figure 5*: Hourly mean leaf temperatures for* Hoheria angustifolia *on the Port Hills, Canterbury, sampled* 95 *cm from the ground every 60 seconds from* 22 *July to* 27 *July* 1989*. (a) Temperatures of external juvenile leaves (three replicates). (b) Difference between internal juvenile (three relicates) and external juvenile leaves. A positive difference means the internal leaves were warmer. (c) Difference between external juvenile and external mature leaves (three replicates). A positive difference means the juvenile leaves were warmer.*

Leaf temperatures during frosts

During the week of 22nd July, external juvenile leaf temperatures fell to nearly - 3°C (Fig. 5a). Internal juvenile leaves were warmer by 0.3 to 0.5°C overnight (Fig. 5b). However, external juvenile leaves were 0.5 to 1.0°C warmer than mature leaves at the same height (Fig. 5c; note the change of scale). High mature leaves (at 250 cm) were normally 1 to 2°C warmer than low mature leaves, due to temperature stratification.

Discussion

Internal vs external leaf temperatures

Bannister and Lee (1989) found that temperatures below - 9°C caused leaf damage in C. *propinqua,* which is consistent with the present study.

During frosts at Cass, differences in temperature between particular *Coprosma* leaves were consistent over the study period. However, internal leaves were not consistently warmer than external leaves. Only those leaves well within the interior of the plants showed much difference from external temperatures. Observations at the time of where ice was forming supported this conclusion. The lack of a consistent difference at the chopped site may be because all the leaves measured at that site were within 10-15 cm of the top of the plants. The zone of temperature amelioration may be limited to further down the plant. Unfortunately for the climate hypothesis, this suggests that most of the leaves which have access to full sunlight and most of the active growing points derive little benefit from any improved microclimate. However, in the top pair of leaves in the RH site, at 165 cm height, the internal leaf was still consistently warmer. This stresses again that much of the variation in leaf temperature at Cass was unexplained.

In any case, the temperature differences found at Cass were very small (less than 0.3°C, while the minimum leaf temperature was - 9.5°C). On the Port Hills, larger differences (up to 0.5 °C) were found in *Hoheria angustifolia*. The leaves used on *Hoheria* were low down on plants 2.5 m tall, and thus there was better shelter from the cold night sky than in the upper part of the *Coprosma* bushes, which were only 90 to 170 cm tall. These differences are still much less than have been reported both locally (Wardle (1985, his Fig. 13) reported a difference of 2°C between the top and bottom of a *Coprosma 'parviflora'* plant near Arthur's Pass) and overseas (for example, 4.5°C above external inside the rosette plant *Espeletia schulzii;* Hedburg and Hedburg, 1979).

The temperature levels, and standard deviations of temperature, show that there is sometimes an effect of position on temperature within divaricate plants. However, this effect is inconsistent and small, especially within the rather open *Coprosma propinqua* bushes. Other unidentified factors (possibly including some more detailed index of leaf exposure) are as important in determining relative leaf temperature during frosts.

Data from calm sunny periods at Cass gave no support to the idea that the tangled branches serve as a heat trap; internal leaves were usually colder than external leaves.

Humidity

The humidity data are not as detailed as those on temperature, due to the larger size of the available sensors. The overall results seem to be similar to those for temperature, i.e. that there is a difference between the inside and outside of a divaricate plant, but the effect is rather small.

Heteroblastic leaf shapes

The Port Hills site showed a surprisingly large difference between the temperatures of external juvenile (small) leaves and adjacent mature (large) leaves. However, this may be partly an artifact of the need to tie down branches to get the mature leaves lower. The result of this manipulation is that the juvenile leaves arc on the side of a tall plant, facing outwards, while the mature leaves are on the side of a horizontal (tied-down) branch, facing outwards and upwards. The data from Cass suggest that such subtle variations in the exact position of a leaf may have a large effect on its relative temperature.

The climate hypothesis evaluated

It seems clear that no heat trap effect was operating, at least in *Coprosma propinqua,* on calm sunny days in winter. However, the data on protection from frost and dehydration are more ambiguous.

Taken on their own, the physical measurements of temperature and humidity seem to show too little difference for the divaricate habit to afford much protection against frosts and drying winds. However, the data on leaf damage (presumably due to frosts) from Cass showed a clear increase in leaf damage on the outside of the *Coprosma* bushes. Even more significantly, the newly-exposed leaves suffered very high levels of damage, as would be predicted if the damage was due to frosts, and the interior of the plant has a less severe climate, hence less frost hardening had taken place inside the plant. This suggests several possibilities:

(1) The small temperature differences measured are just enough to make the difference between frost-damaged leaves and undamaged leaves (unlikely, since the direction of the difference was not consistent).

(2) Fixing thermocouples to small leaves alters their temperature regime, preventing a realistic assessment of their temperatures.

(3) Some variable, other than temperature or gross humidity, is the key climatic factor.

Therefore, it is not possible to completely support or refute the climate hypothesis from these data. We can only hope that these results will stimulate further experimental work aimed at resolving this uniquely New Zealand puzzle. This study also shows the importance of using the plants themselves to indicate when significant changes to the micro-environment have occurred.

Acknowledgements

We thank Graeme Young, for first suggesting decapitating devaricate shrubs, and for help with field work; Andy Sturman for providing climate data from Chilton Valley; and Peter Wardle, Bill Lee and an anonymous referee for helpful comments on the manuscript. The dataloggers were purchased with a University Grants Committee research grant.

References

Allan, H.H. 1961. *Flora of New Zealand, Volume* 1. Government Printer, Wellington. 1085 pp.

Atkinson, I.A.E.; Greenwood, R.M. 1989. Relationships between moas and plants. *In:* Rudge, M.R. (Editor) *Moas, mammals and climate in the ecological history of New Zealand.* Christchurch: New Zealand Journal of Ecology 12 (Supplement).

Bannister, P; Lee, W.G. 1989. The frost resistance of fruits and leaves of some *Coprosma* species in relation to altitude and habitat. *New Zealand Journal of Botany* 27: 477-479.

Bulmer, G.M. 1958. A key to the divaricating shrubs of New Zealand. *Tuatara* 7: 48-61.

Burrows, C.J. 1977. *Cass: history and science in the Cass District, Canterbury, New Zealand.* Botany Department, University of Canterbury, Christchurch. 418 pp.

Burrows, C.J. 1980. Some empirical information concerning the diet of moas. *New Zealand Journal of Ecology 3*: 151-153.

Burrows, C.J.; McCulloch, B.; Trotter, M.M. 1981. The diet of moas based on gizzard contents samples from Pyramid Valley, North Canterbury and Scaifes Lagoon, Lake Wanaka, Otago. *Records of the Canterbury Museum* 9: 309-336.

Burrows, C.J. 1989. Moa browsing: evidence from the Pyramid Valley mire. *In:* Rudge, M.R. (Editor) *Moas, mammals and climate in the ecological history of New Zealand.* Christchurch: New Zealand Journal of Ecology 12 (Supplement).

Campbell Scientific 1986. *CR21X Micrologger Instruction Manual.* Campbell Scientific Inc., Logan, Utah. 229 pp.

Cockayne, L. 1912. Observations concerning evolution, derived from ecological studies in New Zealand. *Transactions and Proceedings of the New Zealand Institute 44*: 1-30.

Dawson, J. 1988. *Forest vines to snow tussocks: the story of New Zealand plants.* Victoria University Press, Wellington. 264 pp.

Diels, L. 1897. Vegetations-Biologie von Neu-Seeland. *Botanische Jahrbucher fur Systematick, Pflanzengeschichte und Pflanzengeographie 22*: 202-300.

Greenwood, R.M.; Atkinson, I.A.E. 1977. Evolution of the divaricating plants in New Zealand in relation to moa browsing. *Proceedings of the New Zealand Ecological Society 24*: 21-33.

Hedberg, I.; Hedberg, O. 1979. Tropical-alpine life forms of vascular plants. *Oikos* 33: 297-307.

McGlone, M.S.; Webb, C.J. 1981. Selective forces influencing the evolution of divaricating plants. *New Zealand Journal of Ecology 4*: 20-28.

Oke, T.R. 1978. *Boundary layer climates.* Methuen, London. 372 pp.

Tomlinson, P.S. 1978. Some qualitative and quantitative aspects of New Zealand divaricating shrubs. *New Zealand Journal of Botany 16*: 299-309.

Tucker, J.M. 1974. Patterns of parallel evolution of leaf form in new world oaks. *Taxon 23*: 129-154.

Wardle, P. 1985. New Zealand timberlines. 2. A study of forest limits in the Crow Valley near Arthur's Pass, Canterbury. *New Zealand Journal of Botany 23*: 235-261.