BioOne COMPLETE

Wind Distortion in Alpine and Subantarctic Plants is Constant among Life Forms but does not Necessarily Reflect Prevailing Wind Direction

Authors: Fitzgerald, Nicholas B., and Kirkpatrick, James B.

Source: Arctic, Antarctic, and Alpine Research, 49(4) : 521-535

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/AAAR0016-054

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Arctic, Antarctic, and Alpine Research, Vol. 49, No. 4, 2017, pp. 521–535
DOI: http://dx.doi.org/10.1657/AAAR0016-054

Wind distortion in alpine and subantarctic plants is constant among life forms but does not necessarily reflect prevailing wind direction

Nicholas B. Fitzgerald[1,*], and James B. Kirkpatrick[1]

[1]Geography and Spatial Sciences, School of Land and Food, University of Tasmania, Private Bag 78, Hobart, TAS 7001, Australia
[*]Corresponding author's email: Nicholas.Fitzgerald@utas.edu.au

A B S T R A C T

Woody plants in windy environments have been used as indicators of prevailing wind direction, because wind can influence plant growth form. We investigated whether non-woody plants also display consistent prevailing wind deformation by observing the direction of asymmetry in growth form of cushion plants, graminoids, and prostrate shrubs growing in highly wind-exposed treeless environments in alpine Tasmania and subantarctic Macquarie Island. Wind distortion of individual plants was inferred from vertical photographs of feldmark and alpine heath vegetation. High correspondence in growth direction between plants of different types suggests a uniform wind influence on plants at the local scale (within <2 m). Dominant wind direction inferred from plant distortion was not consistent with the strongest and most frequent winds. On a relatively dry mountain with shallow soils the plants responded to strong northwest winds in an apparent desiccation response. Elsewhere, they responded to strong southwest winds in an apparent ice abrasion response. We conclude that, in maritime alpine and subantarctic environments, the direction of wind distortion can be measured using any of shrubs, graminoids, or cushion plants, but that this direction is not necessarily a response to the prevailing strongest winds, but rather winds that most damage foliage, the cause of damage varying with environmental context.

Introduction

An influence of wind on plant growth form is observable in many plants, including tropical trees (Noguchi, 1979), subalpine conifers (Wooldridge et al., 1996), and grasses (Aston and Bradshaw, 1966). Deformation of trees and shrubs in windy environments is used as an indicator of prevailing wind direction and wind speeds, providing a useful proxy measure in areas lacking in meteorological data or where winds are variable because of complex topography (Noguchi, 1979; Wooldridge et al., 1996). However, it is not clear whether non-woody plants give the same indication of variation in wind speed and direction as woody plants, or whether the relationship of distortion to particular parameters of wind regimes is constant between environments.

The local wind regime (frequency, magnitude, duration, direction, seasonality), small-scale differences in air flow due to topography and vegetation, other climatic factors, plant morphology, and plant ecophysiology, can influence patterns of plant growth (Anten et al., 2010; Holtmeier and Broll, 2010; Gardiner et al., 2016). Asymmetry in trees exposed to strong winds can occur by physical damage (wind or wind-blown particles) or asymmetric growth due to biomechanical properties of wood under stress (Telewski, 2012). Asymmetry in trees is related to persistent or repeated winds over a certain threshold speed during infrequent synoptic scale weather (Robertson, 1994; Bonnesoeur et al., 2016).

In many cases, high wind speeds reduce transpiration and evaporation by cooling the leaf surface and thus reducing the leaf-to-air vapor pressure deficit (Dixon and

© 2017 Regents of the University of Colorado – 1523-0430/02 $7.00

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Grace, 1984). Whereas wind is unlikely to contribute directly to desiccation, other mechanisms of drought damage are evident in cold climate plants, including cuticular damage caused by windblown particles which can lead to water loss from the leaf. Where water availability is limited, desiccation can lead to foliage loss or mortality. For example, winter water deficits are associated with some northern hemisphere alpine treelines (Holtmeier and Broll, 2010). Cold dry southwest winds, rather than the stronger moister northwest winds, are associated with drought damage to cushion plants on subantarctic Marion Island (le Roux et al., 2005). Subantarctic cushion plants (*Azorella* spp.) are predisposed to desiccation as a result of a simple vascular system, shallow roots, and a structural reliance on turgidity (Bergstrom et al., 2015).

Physical asymmetry in the vegetation drives migration or cyclic succession as plants grow preferentially in the direction of the prevailing wind, with erosion or leaf mortality on the windward side (Ashton and Gill, 1965; Barrow et al., 1968; Mark and Bliss, 1970; Morgan et al., 2010). Wind damage in plants can occur at the patch or landscape scale as distinctive vegetation patterns, such as 'fir wave' forests (Foster, 1988), 'ribbon forests' (Holtmeier and Broll, 2010), dynamic feldmark (Barrow et al., 1968), and vegetated stripes in arid shrublands (Okin and Gillette, 2001). Wind exposure can influence alpine treelines, with woody vegetation limited to lower elevations on slopes subject to stronger winds (Wagemann et al., 2015).

Morphological responses of non-woody plants to wind may be useful as an indicator of wind regimes in areas lacking both meteorological instrumentation and woody vegetation, such as the subantarctic islands. The way in which wind influences plant growth is also of ecological interest, particularly in a rapidly changing climate.

In locations where wind is a key environmental stress we expect that graminoids and cushion plants will display a morphological response to wind by directional growth away from the direction of the strongest winds, as is known to occur in woody plants. Alpine sites in Tasmania where woody plants co-occur with graminoids and/or cushion plants allowed us to investigate whether these three different life forms displayed a consistent directional response within and between sites.

Based on the response of Tasmanian alpine plants, we extend this method beyond the limits of woody plants in the high latitudes of the subantarctic by investigating cushion plants and graminoids on Macquarie Island. We consider the use of non-woody plants as a proxy for wind exposure and their relationship to wind regimes in mid- to high-latitude oceanic climates. To explain the apparent wind response in plants we consider wind characteristics including frequency, intensity, seasonality, air temperature, and relative humidity.

Methods

Three alpine locations in southern Tasmania, Australia, and one study site on the Australian subantarctic territory of Macquarie Island (Fig. 1; Table 1) were examined using vertical photography with a handheld camera. Mount Wellington was rephotographed monthly over one year to test for seasonal changes in plant distortion, while the other locations utilized photography from a single time period. Nomenclature follows de Salas and Baker (2015).

This study derives new data by reanalysis of photographs from previous photo-monitoring studies, plus a new site at Mount Wellington. Consequently, the sampling methods and quadrat sizes vary among sites. However, the quantitative data used here is not area based and therefore not influenced by quadrat size; rather, it is the relative proportion of quadrats at each site with plants present in each wind distortion class. Quadrat sizes (range: 1 m^2–4 m^2) are appropriate for the low alpine vegetation.

In cushion plants, the wind response is evident as foliage death and erosion of the cushion on a particular side of the cushion, typically resulting in a crescent shape (Fig. 2, part a). Cushion plants are variable in shape because of endogenous processes of coalescence and senescence (e.g. Cerfonteyn et al., 2011) as well as environmental factors. We focused only on physical damage consistent with wind impacts. In shrubs there is often wind damage evident as stripped bark, but the key feature is the strongly linear orientation of branches and foliage (Fig. 2, part b). Graminoids that would have a circular or spherical form in sheltered sites can display an asymmetric form indicative of wind distortion, or the leaves and culms are consistently aligned in one direction (Fig. 2, part b).

Twelve 1 × 1 m quadrats were established on a slightly elevated rocky area near the summit of Mount Wellington, chosen because it is exposed to winds from all directions. Quadrats placed at a randomly located northwest corner point were aligned to magnetic north. Random quadrats were excluded if they did not contain both woody plants and graminoids with at least one individual of either displaying directional distortion until 12 quadrats meeting these criteria were established. Each quadrat was photographed vertically (from above) with a wide-angle lens.

This site is located on Jurassic dolerite with regosols (Kirkpatrick and Dickinson, 1984) and includes rock outcrops where soil is confined to joints in the rock.

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

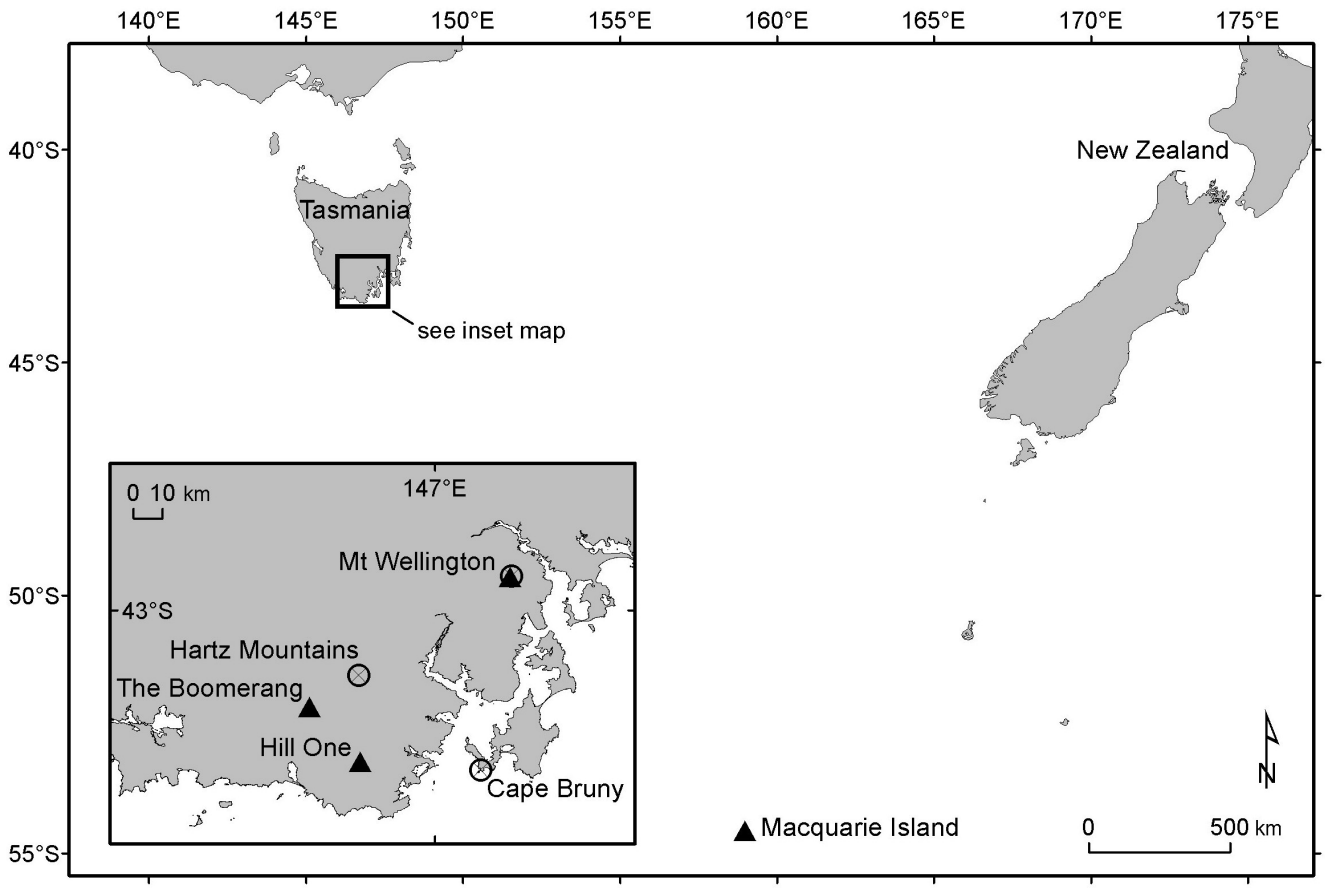


FIGURE 1. Location of the four study sites with the three Tasmanian alpine sites shown in inset map (triangles). Australian Bureau of Meteorology (BOM) weather stations used for wind data also shown for Tasmania (circles). Macquarie Island BOM station not shown due to map scale.

TABLE 1

Study site details. Annual mean air temperature is from a BIOCLIM model for Tasmania (Landscape Logic, 2008) and, for Macquarie Island, from a global BIOCLIM data set (Hijmans et al., 2005). Modeled annual rainfall is derived from Nunez et al. (1996) for Tasmania and Hijmans et al. (2005) for Macquarie Island.

Site	Elevation (m a.s.l.)	Latitude/ Longitude	Number of quadrats	Quadrat size (m)	Modeled annual rainfall (mm)	Mean minimum temp. coldest month (°C)	Mean maximum temp. warmest month (°C)
Mount Wellington	1250–1255	42°54′S 147°14′E	12	1 × 1	925	–1	12
Hill One	990–1010	43°28′S 146°46′E	31	1 × 1.5	1915	0	13
The Boomerang	1030–1081	43°18′S 146°37′E	62	1 × 1	2100	–1	13
Macquarie Island	170–340	54°32′S 158°54′E	35	2 × 2	960–1040	0	7

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

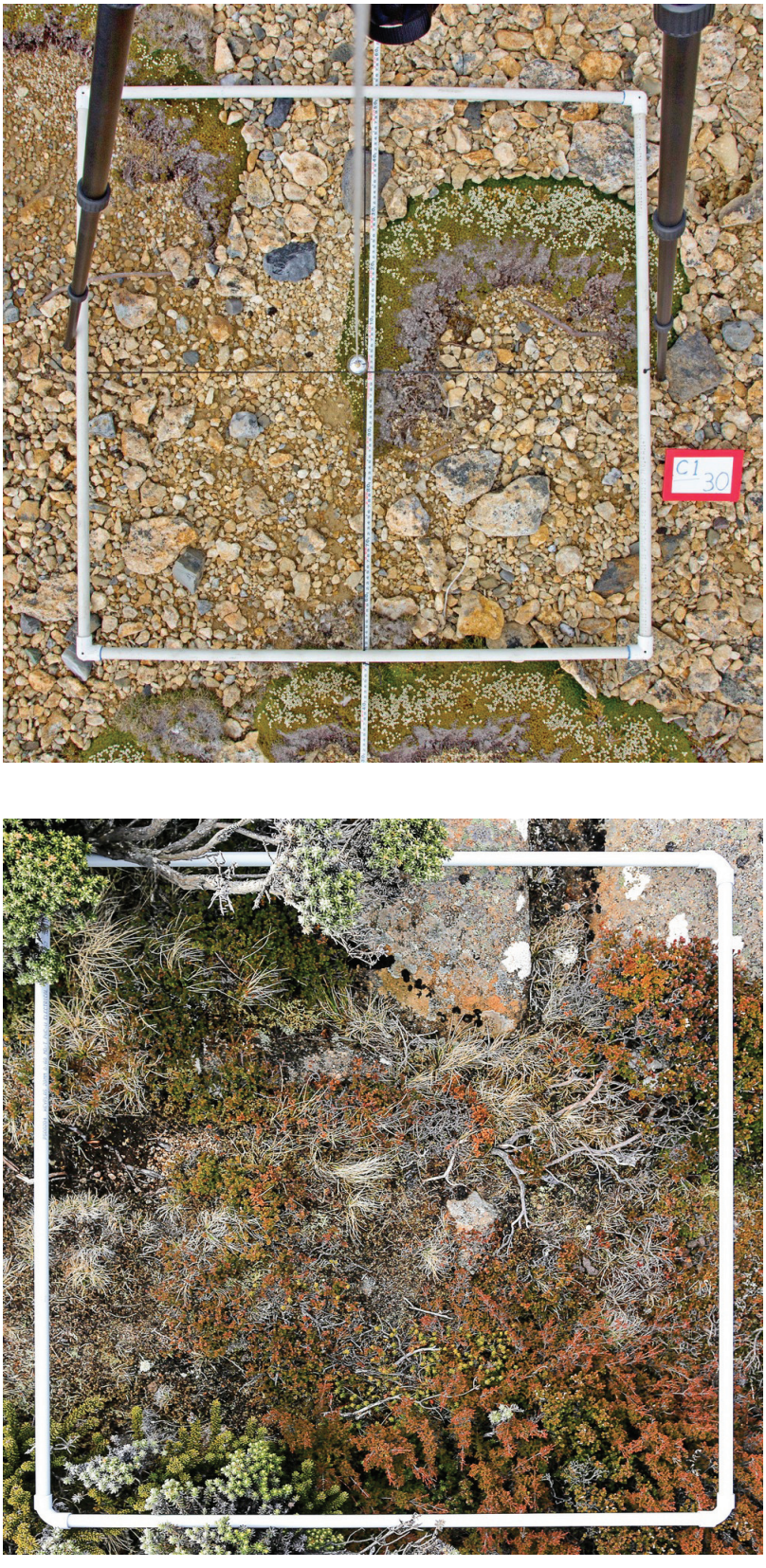


FIGURE 2. (a) Cushion plant *Donatia novae-zealandiae* displaying crescent shape because of wind erosion by southerly winds at The Boomerang. Measuring tape aligned north-south with north at top. Quadrat measures 1 × 1 m. Photograph by Micah Visoiu. (b) Graminoid *Carpha alpina* showing distortion attributed to westerly winds at Mount Wellington. The shrubs *Epacris serpyllifolia* and *Leptospermum rupestre* display similar orientation. Top of image is north. Quadrat measures 1 × 1 m.

Vegetation is alpine heath with an open shrub layer and a mix of graminoids (principally *Carpha alpina*), bryophytes, and forbs. Prostrate and semi-prostrate shrubs include *Leptospermum rupestre* and *Epacris serpyllifolia*, whereas *Richea scoparia* and *Orites acicularis* grow as erect shrubs to around 0.8 m tall.

Individual plants of both shrubs and graminoids were selected from the photographs for analysis if they

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

displayed signs of directional growth (in quadrats with one or fewer individuals of either shrubs or graminoids displaying distortion, other individuals with no distortion were randomly selected to be included in the analysis).

Photographs were rectified to remove lens distortion using GIMP 2.0 (http://www.gimp.org). ScreenScales software (http://www.littlearea.com) was used to measure the dominant compass direction of growth in each graminoid and shrub, and these angles were converted to true north prior to statistical analysis. Each photograph in the time series was visually compared with the original quadrat photograph to determine any change in growth direction for the selected shrubs and graminoids over time.

The second study area was The Boomerang, an extensive sedimentary peak with well-formed stone steps supporting one of the largest feldmarks in Tasmania (Kirkpatrick and Harwood, 1980; Visoiu, 2014). A total of 62 quadrats (each 1 × 1 m) were placed at 5 m intervals (or at vegetation boundaries) along 5 transects in January 2013 (Visoiu, 2014). Transects were oriented both along the major axes of the summit plateau, capturing the highest and flattest parts of the peak, and perpendicular to these to sample different aspects of the higher slopes.

All plants evidently deformed by wind were classified according to which of the eight ordinal and cardinal compass directions describe the directional response. Because of difficulties determining what is an individual in cushion plants, graminoids, and prostrate shrubs, the number of plants was not quantified; rather, a presence/absence of plants in each combination of growth form category (shrub/graminoid/cushion) and wind distortion category (eight compass sectors) was recorded for the quadrat. Where a quadrat contained life forms displaying more than one distortion direction (e.g., cushion plants with both southerly and southwesterly responses and shrubs with southerly and northwesterly responses), we recorded all categories that were present.

Hill One is a terraced sedimentary outcrop in the Southern Range, where feldmark vegetation on the most wind-exposed sites grades into bolster heath and alpine heath (Lynch and Kirkpatrick, 1995). Hill One is a rounded peak with exposure to winds from all directions. Quadrats 1 × 1.5 m were located along north-south and east-west transects and photographed in 1989 and 1998 (Lynch and Kirkpatrick, 1995; Kirkpatrick et al., 2002a). This design samples the highest slopes of the peak with transects radiating in four directions from the summit. Photographs of the 32 quadrats that contained plants with distortion in 2013 were examined and recorded as for The Boomerang site.

Wind damage to *Azorella macquariensis* cushion plants on subantarctic Macquarie Island was recorded by Whinam et al. (2014). These data provide counts of the incidence of directional damage for 234 individual cushions within thirty 2 × 2 m quadrats located in feldmark vegetation on mineral soils developed on igneous geology. In the present study, photographs of the quadrats were reexamined to record presence of wind-distorted grass (*Agrostis magellanica*), in addition to cushion plants, in the eight compass directions, as for the Hill One and Boomerang sites.

Given the potential mechanistic link between snow weather and plant distortion (windblown ice and snow as abrasive agents, breakage of frozen leaves and stems; and conversely protection afforded by snow cover) we sought relevant data on snow cover, with no success. To address this data gap, satellite images of Tasmania from the Landsat archive (1983–2014) were inspected and where widespread snow cover was visible in an image, the synoptic weather pattern was inferred if possible (determined as the direction of cirrus clouds or perpendicular to the orientation of rows of lenticular clouds associated with mountain waves).

Statistical Methods

Meteorological data from the Commonwealth Bureau of Meteorology were obtained for stations relevant to each site (Table 2). To characterize wind regimes, seasonal and directional variation in wind speed, air temperature, and relative humidity were examined using ANOVA. All statistical analyses were performed in R 3.2 (R Core Team, 2014).

For the Mount Wellington data, the mean distortion direction of the distorted plants was calculated using circular statistics. Watson's two sample test of homogeneity for circular data was used to compare the shrub and graminoid populations using the 'circular' package (version 0.4-7) for R (Agostinelli and Lund, 2013). Within each quadrat, individual graminoids and shrubs were randomly selected and paired for a paired *t*-test to compare differences in growth direction between shrubs and graminoids (growth direction data were taken from the first month of the time series because there was little difference between months).

To test whether directionality in plants differed between life-forms at each site we tabulated the frequency of quadrats by the presence of plants in the eight directional distortion classes for each of the two or three life forms present. We used the chi-squared statistic, with Monte Carlo simulation (10,000 replicates), for data sets where small expected values occur. Similarly, we tested for independence between quadrat

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 2

Weather station details.

Weather Station	Elevation (m a.s.l.)	Latitude/ Longitude	Distance from study site	Mean maximum temperature warmest month (°C)	Mean minimum temperature coolest month (°C)	Mean daily wind run (km)
Mount Wellington	1260	42.90°S 147.24°E	<1 km	13.7	–1.7	759
Hartz Mountains	831	43.20°S 146.77°E	Boomerang 16 km Hill One 29 km	17.7	1.4	570
Cape Bruny	55	43.49°S 147.14°E	Boomerang 48 km Hill One 30 km	18.6	6.2	510
Macquarie Island	6	54.50°S 158.94°E	2–16 km	8.8	1.5	749

aspect and plant distortion by tabulating frequency of quadrats by quadrat aspect (east/south/west) and presence of distorted plants (all life forms) for the Hill One site where each of the three transects (excluding the north transect, which comprises only two quadrats) has a distinct aspect. No aspect was recorded or analyzed for Mount Wellington quadrats because these were located on flat ground.

For The Boomerang and Macquarie Island data sets we used binary logistic regression to test whether the aspect of each quadrat predicted the presence/absence of plants in a particular distortion class. To avoid using a circular variable we converted aspect in degrees to radians and calculated the sine and cosine to generate two indices ('eastness' and 'northness,' respectively) to use as independent variables for each quadrat. Macquarie Island quadrats were geographically widely distributed, so we used slope angle and elevation (derived from a 5 m DEM using ArcGIS 10.1) as additional explanatory variables in the model. This test was repeated for each of the distortion directions for each life form (provided there were a minimum of three quadrats with distorted plants).

The frequency of quadrats (classified into eight compass sectors by quadrat aspect) was tabulated by the presence of *Azorella* plants within each of the distortion classes (also classified into eight compass sectors). After excluding rows or columns totaling zero, this contingency table was used to perform a chi-squared test with simulated *p*-value to investigate whether directional wind damage is independent of quadrat aspect. The same test was performed for *Agrostis* plants. Similarly, a chi-squared test was used to compare the frequency of damage to individual cushion plants with the frequency of wind using the same eight compass sectors.

Results

The prevailing winds on Mount Wellington are from southwest to northwest with westerly winds the most frequent and strongest (Fig. 3). Strong warm winds are associated with northwesterly airflows, while southwest winds are slightly colder than other directions at moderately high speeds (see Appendix). Relative humidity varies with wind direction and month (ANOVA, $p < 0.001$), with drying winds typically northwest (Fig. 4) and in the summer months. High temperatures combined with low humidity occur with flows from the west through north between December and February.

Statistically significant variation in air temperature, relative humidity, and wind speed occurs with changes in wind direction and month at all meteorological stations. Of the 93 Landsat images in which snow was visible, the prevailing wind direction was clearly apparent in 40 cases (see Appendix). Southwest winds accounted for the majority of clearly apparent wind patterns where snow cover was present (25 out of 40 images). We therefore surmise that the prevailing winds during periods of widespread alpine snow cover are from the southwest.

On Mount Wellington, both shrubs and graminoids appear to be influenced by west and northwest winds, but not southwest winds (Fig. 3). Mean values for growth direction are similar for shrubs (circular mean = 293°, circular SD = 0.429, $n = 22$) and graminoids (circular mean = 296°, circular SD = 0.541, $n = 33$), with graminoids being more variable. The growth direction for the two groups, shrubs and graminoids, are not significantly different (Watson's U2 0.1283, $p > 0.1$). The mean difference between 19 shrub/graminoid pairs of 5.7° at the initial survey suggests the

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

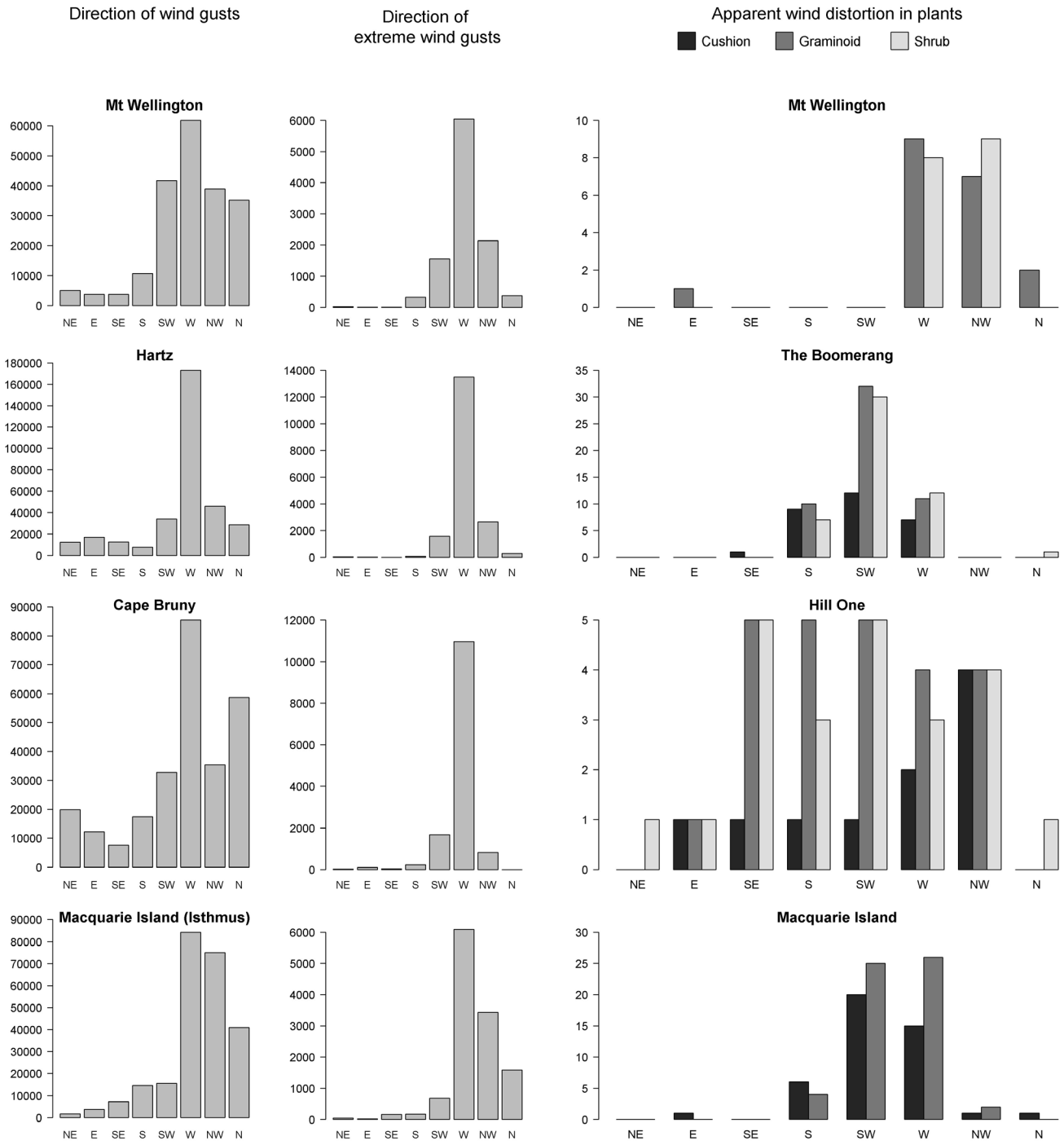


FIGURE 3. Frequency of 10-minute highest wind gusts grouped by wind direction for the four weather stations. Extreme wind gusts are the highest 5% of recorded wind speeds for each station. Direction of plants: number of quadrats at four study sites with shrubs, graminoids, and cushion plants orientated in response to winds from a particular direction (i.e., with plants growing away from that compass direction).

two life forms are not significantly different in orientation (paired *t*-test, *p*-value = 0.35).

Of the 33 graminoid individuals with a distinct orientation at the first survey: 19 remained unchanged throughout the 12 months, 4 changed orientation slightly (but remained within the same compass sector), 9 became indistinct, and one became obscured by a shrub. In some cases, changes in orientation were temporary. Shrubs displayed no change in orientation over this period.

Winds at Hartz and Cape Bruny are predominantly from the west, particularly the strongest winds (Fig. 3).

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

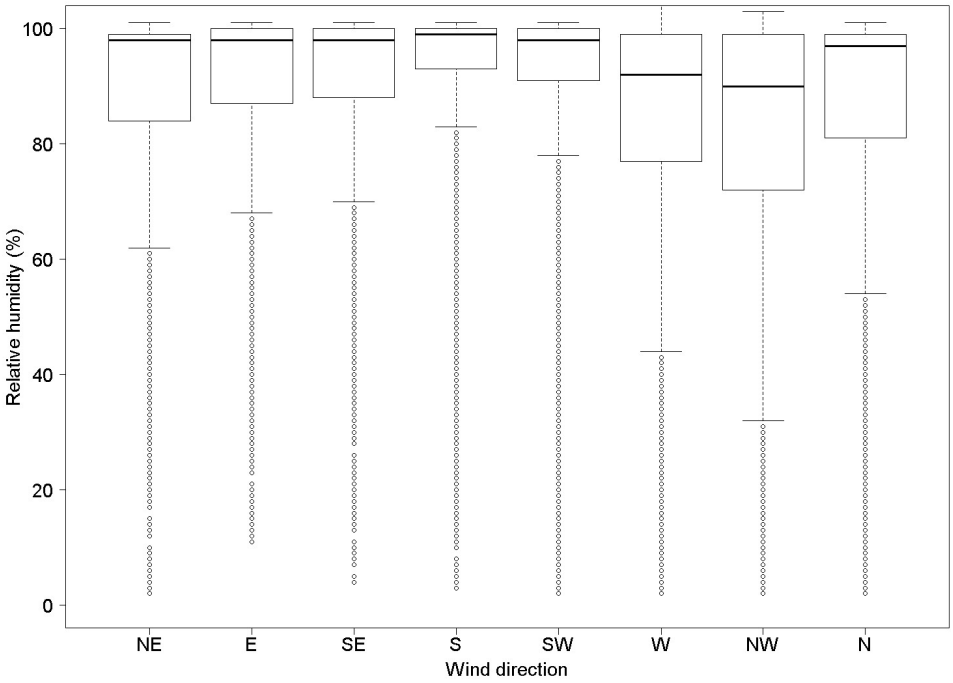


FIGURE 4. Relative humidity at Mount Wellington, 1990–2014. Box and whiskers are quartiles, black line is median, outliers shown as points where they are less than the lower quartile minus 1.5 times the interquartile range.

Given this consistent trend between weather stations at different locations and elevations, these winds are likely to be representative of the wind regimes experienced at The Boomerang and Hill One. This is supported by wind data recorded at Hill One by Lynch and Kirkpatrick (1995) over a relatively short period (April–October 1989) in which west winds were the most frequent and strongest.

Most plants of all three life forms that displayed wind influence at The Boomerang were within the westerly through southerly range, with southwesterly being most frequent (Fig. 3). Of the 62 quadrats, 10 had very little or no vegetation, 8 had vegetation with no apparent wind influence, and 16 had only one life form displaying wind distortion. The remaining 28 quadrats, which contained more than one life form with obvious wind distortion, showed consistency between two or three life forms in all but four cases (Table 3). We did not detect a significant relationship between quadrat aspect and the orientation of plants (chi-squared test, $p = 0.177$). Shrubs with southwesterly distortion were the only subset of plants to display a statistically significant relationship with site aspect (binary logistic regression, eastness $p = 0.034$), reflecting the relative abundance of southwesterly distorted shrubs on west-facing slopes.

Orientation of plants at Hill One was more variable and had a more southerly bias, largely ranging from northwest to southeast (Fig. 3). In all but one of the quadrats in which more than one life form displayed wind distortion, the distortion direction was consistent between the two or three life forms (note that distorted graminoids are less frequent than the other life forms in most quadrats). The relationship between quadrat aspect and plant distortion direction was just significant (chi-squared test with Monte Carlo simulation, average p-value ~ 0.05).

At Macquarie Island the dominant winds are from the west through to north, with strong winds typically from the west (Fig. 3). Most quadrats contained cushion plants with southwesterly or westerly damage (Fig. 3). Counts of damage to *Azorella* cushions show that most damage occurs in the southwest sector, not reflecting the frequencies of maximum wind gust direction (Table 4; chi-squared test, $p < 0.001$). Hail does not appear to be important because 83% of hail events occur on days with west or northwest airflows.

Comparison of total numbers of wind distorted *Azorella* and *Agrostis* in the eight principal compass directions shows similar trends between the life forms (chi-squared test with simulated p-value, $p = 0.278$). Both *Azorella* and *Agrostis* orientations appear to be independent of the quadrat aspect (chi-squared tests with simulated p-value, $p > 0.8$). Individual exceptions to this are *Agrostis* with westerly distortion (logistic regression, northness $p = 0.047$) and *Azorella* with southwest distortion (northness $p = 0.024$). Quadrat slope and elevation were not statistically significant in predicted presence/absence of plant distortion.

Discussion

Congruence Between Life Forms in Direction of Distortion

The Mount Wellington, Boomerang, and Hill One data show that shrubs and graminoids have a similar

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 3

Frequency of wind distortion congruence across life forms within 62 quadrats at The Boomerang. Bold numerals are total number of quadrats where the life forms display the same orientation (in at least some individuals), italic numerals are number of quadrats where different life forms display different orientations (no congruence present). Fifteen quadrats that did not contain more than one life form with wind distortion were not scored.

	Shrub	Graminoid	Cushion
Shrub		**19**	**6**
Graminoid	*3*		**18**
Cushion	*0*	*1*	

TABLE 4

Frequency of damage to 234 *Azorella* cushions on Macquarie Island by section of cushion affected (excluding damage in the center). Some cushions have damage in multiple sectors. Data from Whinam et al. (2014). Frequency of daily maximum wind gusts for Macquarie Island is shown classified in the same eight directional classes. Extreme wind gusts are the highest 5% of daily maxima.

Compass sector	Damage count	%	Daily max. wind gust frequency	%	Extreme wind gust frequency	%
NE	21	6.7	189	1.0	0	0.0
E	16	5.1	210	1.1	0	0.0
SE	18	5.8	614	3.1	4	0.4
S	51	16.3	1090	5.5	18	1.8
SW	111	35.6	693	3.5	28	2.7
W	60	19.2	7334	37.0	620	60.4
NW	19	6.1	6264	31.6	281	27.4
N	16	5.1	3421	17.3	75	7.3
Total	312	100	19815	100	1026	100

growth response in a windy environment, indicating that graminoids have potential for use as indicators of wind direction. Distortion of graminoids was generally less distinct than that of shrubs and varied seasonally, becoming most obvious when mature culms were present. Graminoids were less effective than shrubs as indicators of wind regime as a result of a greater variation in their orientation and, in some instances, temporal variation in individuals. However, with a sufficient sample size they provide similar orientation results to woody vegetation.

The data from The Boomerang, Hill One, and Macquarie Island show that cushions and graminoids also have a similar response in a windy environment. Therefore, in the absence of woody plants, either cushions or graminoids can be used to indicate spatial patterns of wind direction. Whereas the likely mechanical processes and morphology of wind distortion vary among the three distinct life forms examined here, their directional responses to damaging winds were consistent.

Wind direction as indicated by vegetation is largely consistent between quadrats at each site. However, the quadrats that do display different wind direction tend to be internally consistent, in that there is congruence in apparent wind response between life forms, suggesting local differences in wind flow related to topography. Several quadrats on flat ground or a variety of aspects provided a signal of prevailing wind direction even if there were some small-scale variability due to topography or vegetation.

Correspondence of Distortion to Wind Regimes

Our data suggest patterns of distortion in alpine and subantarctic plants, regardless of growth form, do not simply relate to the most frequent strong winds, as is generally the case in other environments (Noguchi, 1979; Hadley and Smith, 1983; Robertson, 1986; Wooldridge et al., 1996), with some exceptions, such as seasonality of winds (Holtmeier, 2009).

One possible explanation for this discrepancy is the locations of meteorological stations. The Mount Wellington station is located near the summit with a clear line of view in all directions, so may be reliable. Wind

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

data from the Tasmanian weather stations examined in this study consistently indicate prevailing westerly winds, even at Hartz Mountains where the weather station is located east of a prominent ridge and therefore might be somewhat sheltered.

The weather station at Macquarie Island is located at 6 m a.s.l. and is not directly exposed to southwest winds because of the 200- to 300-m-high adjacent plateau. Nevertheless, wind speed at the meteorological station predicts that at other locations on the island, including at high elevations, where the winds are much stronger than at sea level (Jenkin, 1972; Davies and Melbourne, 1999; Selkirk and Saffigna, 1999; Tweedie, 2000). Jenkin (1972) interpreted an increase in the difference between sea level and plateau wind speeds in October to a high frequency of S and SW winds during this period, suggesting that the meteorological station is not representative of winds from these sectors. Selkirk and Saffigna (1999) found that wind direction on the plateau was very similar to that observed at the meteorological station over the course of one month, but recorded no wind speed data.

In rugged mountain topography we would expect very localized variation in winds, but such variation is unlikely to occur at our Tasmanian study sites. Strong westerly winds were consistently recorded from Tasmanian stations. Short-term wind data from the Hill One site (Lynch and Kirkpatrick, 1995) is consistent with data for wind speed and direction from both weather stations used in our analysis for this site. Given the similar topography of The Boomerang, we expect the wind regimes from these stations to also be representative of this site. However, the wind experienced by low-growing plants at the ground surface may differ from the wind direction at instrument height, particularly in mountainous terrain. Therefore, meteorological observations may not be representative of the vegetation microenvironment.

The data presented here from the quadrats at Hill One shows much more variable responses of cushion plants and shrubs to wind than the less systematic observations of Lynch and Kirkpatrick (1995, their Fig. 12), who reported distorted cushion plants and shrubs overwhelmingly displaying a distinct southwest to northeast trend in growth. The Maatsuyker Island wind data examined by Lynch and Kirkpatrick (1995) indicates dominant northwesterlies. However, the wind direction data from this station are considered unreliable.

Because southwesterly winds are neither strongest nor most frequent in either the Hill One or Maatsuyker climate data, this growth response is potentially related to low-temperature events, where southwesterlies tend to be stronger than other winds (Lynch and Kirkpatrick, 1995). However, the southwesterly winds are only slightly stronger than other wind directions associated with low temperatures.

In the Tasmanian feldmark sites, the congruence in apparent wind response between shrubs and graminoids or shrubs and cushion plants within individual quadrats suggests that the different vegetation orientation between quadrats is a result of localized differences in wind flow on different aspects of the summit combined with microtopographic effects. Patterns in feldmark may be reinforced by a feedback whereby vegetation modifies surface air flow (Barrow et al., 1968; Selkirk-Bell and Selkirk, 2013).

The major discrepancy in direction of distortion is between our Mount Wellington site and the others. As with our plants at the other sites, the trees in the subalpine forests on Mount Wellington lean away from the southwest (Gilfedder, 1988), whereas, in our quadrats near the summit, the plants lean away from the northwest. Leaf damage from wind-blown ice is greater on the windward (southwest) side of treeline eucalypts, which, combined with the asymmetric crown form, suggests ice-bearing southwesterly winds are the controlling factor (Gilfedder, 1988).

Gilfedder (1988) presents evidence that the upper altitudinal limit of trees on Mount Wellington is related to drought. Hot, dry northwesterly winds occur during the summer growing season. Unlike other Tasmanian alpine regions, Mount Wellington may be subject to the warm dry foehn winds, which can occur in southeastern Tasmania during northwesterly weather (Kirkpatrick et al., 2002b; Sharples, 2009; Fox-Hughes, 2012). Mount Wellington has lower average rainfall than other alpine areas (Nunez et al., 1996) and has shallow soils compared to the other sites; therefore, the alpine vegetation is more likely to be subject to water stress. Further exploration of this water stress theory would require ecophysiological studies of alpine plants at Mount Wellington to measure water potentials.

These northwesterly winds are implicated as a drying force in the complex patterning of migrating *Sphagnum* mires on the Tasmanian Central Plateau (Morgan et al., 2010). We suggest that the direction of asymmetry reflects greater damage from desiccation during northwesterly winds than ice abrasion during southwesterly weather. Our other sites have higher precipitation and deeper soils than those on Mount Wellington (Table 1), making desiccation an unlikely cause of asymmetry.

The lack of a match between the southwesterly trend in wind damage on Macquarie Island, Hill One, and The Boomerang, and the dominant westerly and northwesterly winds, may reflect the frontal synoptic patterns associated with the potential for ice abrasion. Cold

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

fronts bearing snow move in from the west, followed by increasingly southerly cold air as the pressure becomes higher (Jones, 2003). Our satellite image interpretation suggests that snow cover in Tasmania's alpine zone typically coincides with southwesterly weather. Under clear conditions, snow becomes icy as it is transported locally to the northeast, the location of most snow patches (Parry et al., 2016). Apart from these snow patches, which usually are filled with snow through winter and early spring, the vegetation is mostly exposed to wind (Kirkpatrick, 1997). We suggest the correspondence of icy snow with low snow cover and strong winds is maximized with southwesterlies.

While studies of asymmetry in trees typically implicate prevailing winds, cold winds have a greater influence than warm winds (Grace, 1977). Asymmetry in tree crowns can be produced by physical damage on the windward side (such as ice abrasion during glazing storms), but there may also be a microclimatic effect whereby growth rates are higher on the lee side (Foster, 1988).

Wind-blown ice, soil, snow, and salt spray often have a greater influence on plant form than wind per se (Grace, 1977; Ennos, 1997). Similar processes are likely to be involved in the growth of prostrate shrubs in alpine environments, in that a combination of physical damage, differential growth rates, and thigmotropism drive a directional response that may be confounded by factors other than wind speed. Salt spray may be implicated in foliar damage in coastal environments but is unlikely to be a contributing factor in the Tasmanian sites given the elevation and distance from the coast. On Macquarie Island, salt spray does not substantially affect higher elevations (Mallis, 1988).

Studies of the subantarctic cushion plant *Azorella selago* Hook. f. (closely related and morphologically similar to the allopatric Macquarie Island endemic *A. macquariensis*) report asymmetry in microclimates and wind damage. Microclimatic differences in soil moisture and temperature are evident, with greater variation in these factors on the windward (western) side of *A. selago* cushions, apparently because of increased evaporation and less snow accumulation (Haussmann et al., 2009).

In a field experiment with *A. selago* subjected to reduced rainfall, greater senescence on the southwest side of cushions suggests cold dry southwesterly winds have a desiccating effect under drought conditions (le Roux et al., 2005). In contrast to the leeward migration typically observed in feldmark plants, Boelhouwers et al. (2003) reported *A. selago* cushions migrating toward the prevailing wind as a result of decay of the cushions on the leeward side where needle ice forms. On Marion Island, frost events are predominantly associated with southwesterly airflows (Nel et al., 2009). Macquarie Island is likely to experience a similar regime given the similarities in synoptic weather patterns and soil temperatures between it and Marion Island, and thus windblown ice is likely associated with southwesterly winds.

Cold air is dense and more effective at moving particles than warm wind (Selkirk and Saffigna, 1999), which may accentuate the abrasive effects of ice and soil particles, particularly near ground level. The dynamic stress experienced by plants is a function of wind speed and air density (Wagemann et al., 2015) so relatively low elevation locations such as Macquarie Island will experience more damaging winds for a given wind speed.

Active wind erosion of mineral soils on Macquarie Island (Selkirk and Saffigna, 1999) under conditions of frequent strong winds and infrequent snow cover provides suitable conditions for sand-blasting of vegetation, both on the coast and plateau. Hence Macquarie Island vegetation might be more predisposed to wind damage than typical high-latitude and alpine environments where extensive snow cover provides protection from wind for a large part of the year, or Tasmanian alpine vegetation that occurs almost exclusively on dolerite or quartzite peaks with very little sand and gravel. Hill One and The Boomerang are rare examples of sedimentary geology in the Tasmanian alpine zone, which explains the well-developed feldmark on these peaks. Spatial modeling of extreme wind gusts suggests that Hill One is subject to some of the most damaging winds in Tasmania (Cechet et al., 2012).

Conclusions

We conclude that, at least in maritime alpine and subantarctic environments, the direction of wind distortion can be measured using any of shrubs, graminoids, or cushions, but that these directions are not related to any consistent attribute of the local climate. We identify desiccation and ice abrasion as the likely causes of asymmetry at our sites, with the former only on a relatively dry mountain with shallow soils and responding to strong northwesterly winds, and the latter elsewhere, responding to strong southwesterly winds. Thus, plant distortions do not reflect the most frequent strong winds, but rather the most frequent damaging strong winds. The novel use of graminoids to indicate ecologically important wind direction has applications in environments lacking woody vegetation.

Acknowledgments

We thank Paul Fox-Hughes for advice on meteorological factors. Jennie Whinam and Micah Visoiu pro-

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

vided raw data and photographs for The Boomerang and Macquarie Island sites. Macquarie Island fieldwork was supported by the Australian Antarctic Division and the Tasmanian Parks and Wildlife Service.

References Cited

Agostinelli, C., and Lund, U., 2013: *R package 'circular': Circular Statistics (version 0.4-7)*. https://r-forge.r-project.org/projects/circular/.

Anten, N. P. R., Alcalá-Herrera, R., Schieving, F., and Onoda, Y., 2010: Wind and mechanical stimuli differentially affect leaf traits in *Plantago major*. *The New Phytologist,* 188: 554–64.

Ashton, D. H., and Gill, A. M., 1965: Pattern and process in a Macquarie Island feldmark. *Proceedings of the Royal Society of Victoria,* 79: 235–245.

Aston, J. L., and Bradshaw, A. D., 1966: Evolution in closely adjacent plant populations. II. *Agrostis stolonifera* in maritime habitats. *Heredity,* 21: 649–664.

Barrow, M. D., Costin, A. B., and Lake, P., 1968: Cyclical changes in an Australian fjaeldmark community. *Journal of Ecology,* 56: 89–96.

Bergstrom, D. M., Bricher, P. K., Raymond, B., Terauds, A., Doley, D., McGeoch, M. A., Whinam, J., Glen, M., Yuan, Z., Kiefer, K., Shaw, J. D., Bramely-Alves, J., Rudman, T., Mohammed, C., Lucieer, A., Visoiu, M., Jansen van Vuuren, B., and Ball, M. C., 2015: Rapid collapse of a sub-Antarctic alpine ecosystem: the role of climate and pathogens. *Journal of Applied Ecology*, 52, 774–783.

Boelhouwers, J., Holness, S., and Sumner, P., 2003: The maritime Subantarctic: a distinct periglacial environment. *Geomorphology*, 52: 39–55.

Bonnesoeur, V., Constant, T., Moulia, B., and Fournier, M., 2016: Forest trees filter chronic wind-signals to acclimate to high winds. *New Phytologist,* 210(3): doi: http://dx.doi.org/10.1111/nph.13836.

Cechet, R., Sanabria, L., Divi, C., Thomas, C., Yang, T., Arthur, W., Dunford, M., Nadimpalli, K., Power, L., White, C., Bennett, J., Corney, S., Holz, G., Grose, M., Gaynor, S., and Bindoff, N., 2012: *Climate Futures for Tasmania: Severe Wind Hazard and Risk Technical Report*. Canberra: Geoscience Australia, 122 pp.

Cerfonteyn, M. E., le Roux, P. C., van Vuuren, B. J., and Born, C., 2011: Cryptic spatial aggregation of the cushion plant *Azorella selago* (Apiaceae) revealed by a multilocus molecular approach suggests frequent intraspecific facilitation under sub-Antarctic conditions. *American Journal of Botany,* 98: 909–914.

Davies, K. F., and Melbourne, B. A. 1999: Statistical models of invertebrate distribution on Macquarie Island: a tool to assess climate change and local human impacts. *Polar Biology,* 21: 240–250.

de Salas, M., and Baker, M., 2015: *A Census of the Vascular Plants of Tasmania, Including Macquarie Island*. Hobart: Tasmanian Herbarium, Tasmanian Museum and Art Gallery, 147 pp.

Dixon, M., and Grace, J., 1984: Effect of wind on the transpiration of young trees. *Annals of Botany*, 53: 811–819.

Ennos, A., 1997: Wind as an ecological factor. *Trends in Ecology and Evolution,* 12: 108–111.

Foster, J. R., 1988: The potential role of rime ice defoliation in tree mortality of wave-regenerated balsam fir forests. *Journal of Ecology,* 76: 172–180.

Fox-Hughes, P., 2012: Springtime fire weather in Tasmania, Australia: Two case studies. *Weather and Forecasting,* 27: 379–395.

Gardiner, B., Berry, P., and Moulia, B., 2016: Review: wind impacts on plant growth, mechanics and damage. *Plant Science*, 245: doi: http://dx.doi.org/10.1016/j.plantsci.2016.01.006.

Gilfedder, L., 1988: Factors influencing the maintenance of an inverted *Eucalyptus coccifera* tree-line on the Mt Wellington Plateau, Tasmania. *Australian Journal of Ecology,* 13: 495–503.

Grace, J., 1977: *Plant Response to Wind*. London: Academic Press, 204 pp.

Hadley, J. L., and Smith, W. K., 1983: Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, U.S.A. *Arctic and Alpine Research,* 15: 127–135.

Haussmann, N. S., Boelhouwers, J., and McGeoch, M. A., 2009: Fine scale variability in soil frost dynamics surrounding cushions of the dominant vascular plant species (*Azorella selago*) on sub-Antarctic Marion Island. *Geografiska Annaler: Series A, Physical Geography,* 91: 257–268.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and Jarvis, A., 2005: Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25: 1965–1978.

Holtmeier, F.-K., 2009: *Mountain Timberlines: Ecology, Patchiness and Dynamics*. Berlin: Springer, 438 pp.

Holtmeier, F.-K., and Broll, G., 2010: Wind as an ecological agent at treelines in North America, the Alps, and the European Subarctic. *Physical Geography,* 31: 203–233.

Jenkin, J. F., 1972: *Studies on Plant Growth in a Subantarctic Environment*. Ph.D. thesis, University of Melbourne, Melbourne, 297 pp.

Jones, M. C., 2003: Climatology of cold outbreaks with snow over Tasmania. *Australian Meteorological Magazine,* 52: 157–169.

Kirkpatrick, J., 1997: *Alpine Tasmania*. Melbourne: Oxford University Press, 196 pp.

Kirkpatrick, J., and Dickinson, K., 1984: The impact of fire on Tasmanian alpine vegetation and soils. *Australian Journal of Botany,* 32: 613–629.

Kirkpatrick, J., and Harwood, C., 1980: The vegetation of an infrequently burned Tasmanian mountain region. *Proceedings of the Royal Society of Victoria,* 91: 79–107.

Kirkpatrick, J., Bridle, K. L., and Lynch, A., 2002a: Changes in alpine vegetation related to geomorphological processes and climatic change on Hill One, Southern Range, Tasmania, 1989–2000. *Australian Journal of Botany,* 50: 753–759.

Kirkpatrick, J., Bridle, K., and Wild, A., 2002b: Succession after fire in alpine vegetation on Mount Wellington, Tasmania. *Australian Journal of Botany,* 50: 145–154.

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Landscape Logic, 2008: *Project 1 Spatial Database and Analyses*. RMIT University, Melbourne.

le Roux, P. C., McGeoch, M. A., Nyakatya, M. J., and Chown, S. L., 2005: Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biology,* 11: 1628–1639.

Lynch, A. J. J., and Kirkpatrick, J. B., 1995: Pattern and process in alpine vegetation and landforms at Hill One, Southern Range, Tasmania. *Australian Journal of Botany,* 43: 537–554.

Mallis, M. 1988: A quantitative investigation into scavenging of airborne sea salt over Macquarie Island. *Papers and Proceedings of the Royal Society of Tasmania,* 122: 121–128.

Mark, A. F., and Bliss, L. C., 1970: The high-alpine vegetation of Central Otago, New Zealand. *New Zealand Journal of Botany,* 8: 381–451.

Morgan, S. W., Kirkpatrick, J. B., and di Folco, M.-B., 2010: Wind-controlled linear patterning and cyclic succession in Tasmanian *Sphagnum* mires. *Journal of Ecology,* 98: 583–591.

Nel, W., Boelhouwers, J. C., and Zilindile, M. B., 2009: The effect of synoptic weather systems on sub-surface soil temperatures in a diurnal frost environment: preliminary observations from sub-Antarctic Marian Island. *Geografiska Annaler: Series A, Physical Geography,* 91: 313–319.

Noguchi, Y., 1979: Deformation of trees in Hawaii and its relation to wind. *Journal of Ecology,* 67: 611–628.

Nunez, M., Kirkpatrick, J., and Nilsson, C., 1996: Rainfall estimation in south-west Tasmania using satellite images and phytosociological calibration. *International Journal of Remote Sensing,* 17: 1583–1600.

Okin, G. S., and Gillette, D. A., 2001: Distribution of vegetation in wind-dominated landscapes: implications for wind erosion modeling and landscape processes. *Journal of Geophysical Research,* 106(D9): 9673–9683.

Parry, J., Kirkpatrick, J. B., and Marsden-Smedley, J., 2016: Explaining the distribution, structure and species composition of snow-patch vegetation in Tasmania, Australia. *Australian Journal of Botany*, 64: 484–491.

R Core Team, 2014: *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Robertson, A., 1986: Estimating mean windflow in hilly terrain from tamarack (*Larix lancina* (Du Roi) K. Koch) deformation. *International Journal of Biometeorology,* 30: 333–349.

Robertson, A. 1994: Directionality, fractals and chaos in wind-shaped forests. *Agricultural and Forest Meteorology,* 72: 133–166.

Selkirk, J. M., and Saffigna, L. J., 1999: Wind and water erosion of a peat and sand area on Subantarctic Macquarie Island. *Arctic, Antarctic, and Alpine Research,* 31: 412–420.

Selkirk-Bell, J. M., and Selkirk, P. M., 2013: Vegetation-banked terraces on Subantarctic Macquarie Island: a reappraisal. *Arctic, Antarctic, and Alpine Research,* 45: 261–274.

Sharples, J. J., 2009: An overview of mountain meteorological effects relevant to fire behaviour and bushfire risk. *International Journal of Wildland Fire,* 18: 737–754.

Telewski, F., 2012: Is windswept tree growth negative thigmotropism? *Plant Science,* 184: 20–28.

Tweedie, C. E., 2000: *Climate Change and the Autecology of Six Plant Species along an Altitudinal Gradient on Subantarctic Macquarie Island*. Ph.D. thesis, University of Queensland, Brisbane, 334 pp.

Visoiu, M., 2014: *Monitoring of the Expression of Feldmark Vegetation on The Boomerang, Southern Tasmania*. Hobart: Department of Primary Industries, Parks, Water and Environment, Nature Conservation Report 2014/3, 18 pp.

Wagemann, J., Thies, B., Rollenbeck, R., Peters, T., and Bendix, J., 2015: Regionalization of wind-speed data to analyse tree-line wind conditions in the eastern Andes of southern Ecuador. *Erdkunde*, 69: 3–19.

Whinam, J., Abdul-Rahman, J. A., Visoiu, M., di Folco, M.-B., and Kirkpatrick, J. B., 2014: Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. *Australian Journal of Botany,* 62: 10–21.

Wooldridge, G. L., Musselman, R. C., Sommerfeld, R. A., Fox, D. G., and Connell, B. H., 1996: Mean wind patterns and snow depths in an alpine-subalpine ecosystem as measured by damage to coniferous trees. *Journal of Applied Ecology,* 33: 100–108.

MS submitted 6 September 2016
MS accepted 7 July 2017

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix

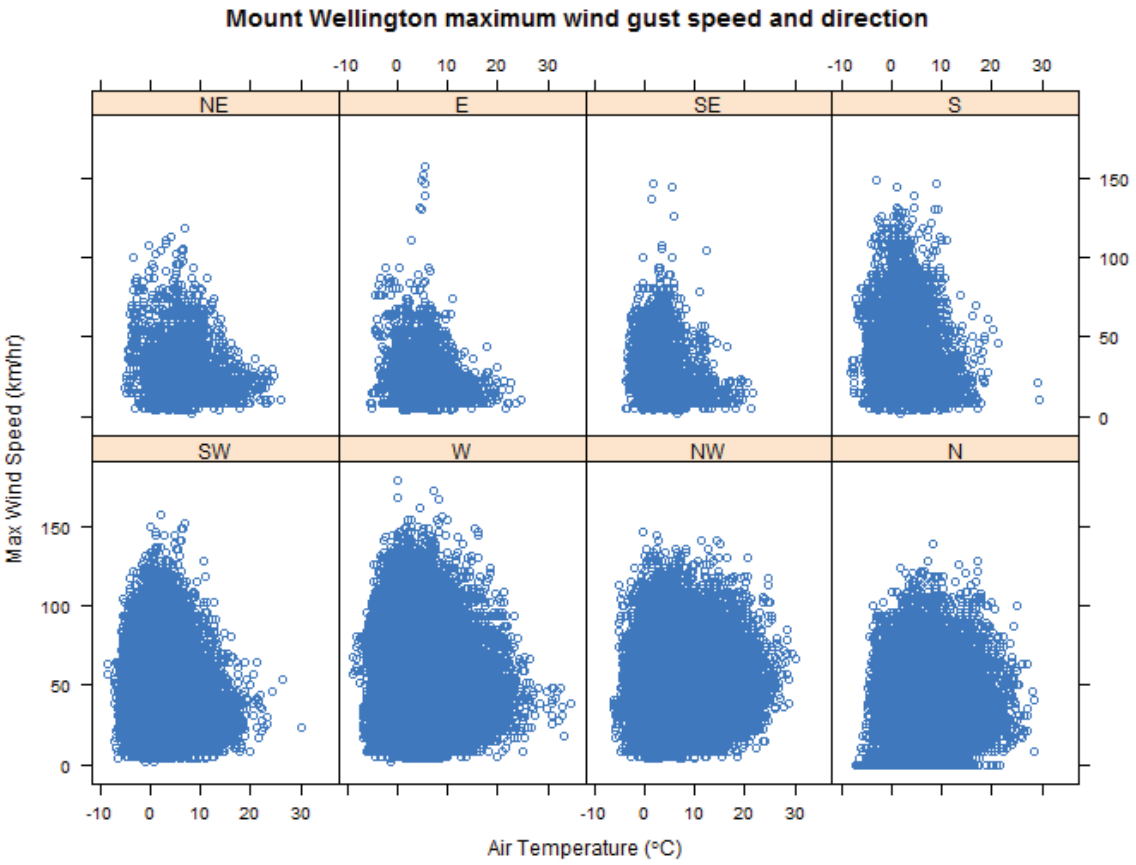


FIGURE A1. Hourly maximum wind speed and air temperature grouped by wind direction at Mount Wellington, 1990–2014.

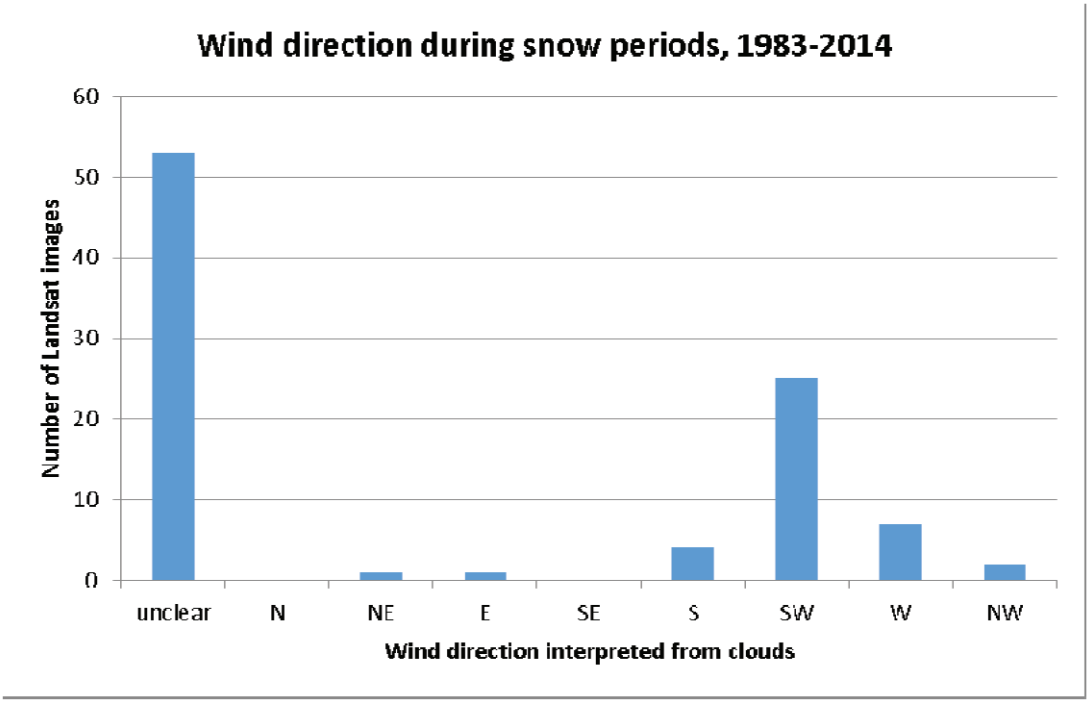


FIGURE A2. Synoptic scale wind flow during times of widespread alpine snow cover visible in Tasmania on Landsat images, 1983–2014.

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE A1

Boomerang logistic regression results: *p*-values for Eastness, Northness, and interaction between Eastness and Northness as predictors of plant orientation. Sample sizes for plants with wind distortion in directions other than west, southwest, and south were too small for this analysis.

		West	Southwest	South
Shrubs	Eastness	0.301	0.034*	0.464
	Northness	0.307	0.650	0.354
	Eastness: Northness	0.301	0.078	0.570
Graminoids	Eastness	0.115	0.129	0.271
	Northness	0.144	0.141	0.274
	Eastness: Northness	0.633	0.154	0.255
Cushions	Eastness	0.407	0.406	0.899
	Northness	0.512	0.557	0.184
	Eastness: Northness	0.525	0.387	0.754

* = significance at $p < 0.05$.

TABLE A2

Macquarie Island logistic regression: *p*-values for Eastness, Northness, and interaction between Eastness and Northness as predictors of plant orientation. Sample sizes for plants with wind distortion in directions other than west, southwest, and south were too small for this analysis.

		West	Southwest	South
Cushions	Eastness	0.892	0.472	0.951
	Northness	0.641	0.024*	0.095
	Eastness: Northness	0.212	0.719	0.333
Graminoids	Eastness	0.231	0.392	0.318
	Northness	0.047*	0.636	0.128
	Eastness: Northness	0.842	0.763	0.227

* = significance at $p < 0.05$.

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use