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Tree-Limit Ribbons in the Snowy Mountains, Australia: Characterization and Recent Seedling Establishment

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Abstract

Tree-limit ribbons, isolated ribbons of trees growing above, but close to the alpine tree limit, have been described previously only for North America. Here, we describe such ribbons from the Snowy Mountains, Australia. Spread of trees above the treeline on lee slopes is generally as ribbons perpendicular to the prevailing wind, with snowdrifts accumulating downwind suppressing seedling establishment. The ribbons exhibit long-term stability, with estimated stem ages of snowgum (*Eucalyptus pauciflora* subsp. *niphophila*) up to 500 years, and the lignotubers considerably older. Windblown branches containing viable seed may allow initial establishment of trees above treeline leading to the formation of ribbons. Seedling establishment uphill of the highest ribbons is rare because snowgum has no inherent seed dispersal mechanism, depending on gravity for dispersal. However, seedling establishment immediately downslope of the highest ribbons, normally suppressed by snowdrifts, is more common and appears to have occurred mainly post-1970. Whether seedlings that established under snowdrifts post-1970 will remain as krummholz or proceed to full tree status will depend on the future snow regime and the persistence of regular snowdrifts. However, there are trees that have established below ribbons but outside the influence of snowdrifts, that exist now as younger ribbons, in clumps, or as individuals, in areas that previously did not support trees.

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Introduction

The alpine treeline is a transition zone demarcating the boundary between contiguous woodland or forest and alpine vegetation (Körner, 2003). The location of the treeline is strongly temperature-dependent and occurs where the mean air temperature in the growing season lies between 5.5 and 7.5 °C (Körner, 2003; Körner and Paulsen, 2004). The treeline ecotone in the Snowy Mountains of southeastern Australia (36°27'S, 148°16'E), where snowgum, *Eucalyptus pauciflora* subsp. *niphophila*, predominates, is a fractured zone, generally conforming to an altitude between about 1750 and 2000 m a.s.l. The altitude of the treeline is higher on the warmer northern and western slopes and lower on southern and eastern slopes, which are also in the lee of the prevailing northwesterly winds (Slatyer, 1989; Green and Pickering, 2009a; Green, 2009). Warming of the alpine region of the Snowy Mountains since 1970 at a rate of about 0.2 °C per decade (Hennessy et al., 2003) has made the lowest 100 m of the alpine zone climatically suitable for the growth of trees. However, there has been no detectable altitudinal advance of the Snowy Mountains treeline over the past 100 years (Green, 2009).

Infrequent establishment of seedlings by long-distance dispersal (such as windblown branches containing seed capsules) seems to have occurred above treeline in the Snowy Mountains, with stands of trees at sites much higher than the treeline (Slatyer, 1989). Apart from locations where trees have established upon rocky spurs, forming woodland 'fingers,' isolated pockets of trees above the subalpine woodland on lee slopes assume a linear form, perpendicular to the direction of the prevailing wind. Once trees establish well above the treeline and start trapping drifting snow on their

downwind side, the accumulating snowdrift likely suppresses further seedling establishment downwind (Billings, 1969). The trees in the Snowy Mountains have spread laterally across the slopes forming ribbons, but the mechanism by which this linear pattern forms currently lacks a coherent explanation (Bekker et al., 2009).

Here, we aim to characterize ribbons of trees growing perpendicular to prevailing winds close to the alpine tree limit in the Snowy Mountains. We also investigate the mechanisms for downwind, down slope, seedling recruitment and examine whether canopy removal within the established ribbon after fire can facilitate these processes. In doing this, we aim to determine the factors that underpin the formation of tree-limit ribbons and that have allowed recent seedling establishment.

Methods

For the purpose of this study, we define a 'tree' as a woody plant (either single or multi-stemmed) that achieves sufficient height to project above the average snow cover typical of the specific site (Holtmeier, 2003). Krummholz forms of *E. pauciflora* are rare (Slatyer, 1989) and generally absent above the treeline (K. Green, personal observation) although most trees are multi-stemmed. The terms 'tree limit' and 'species limit' for snowgum are therefore the same within the Snowy Mountains.

RIBBON STUDY SITES

Eleven snowgum ribbons were chosen for study following reconnaissance surveys (Fig. 1, Table 1). To avoid the confounding effects of upwind trees, only the highest ribbons, with no outpost

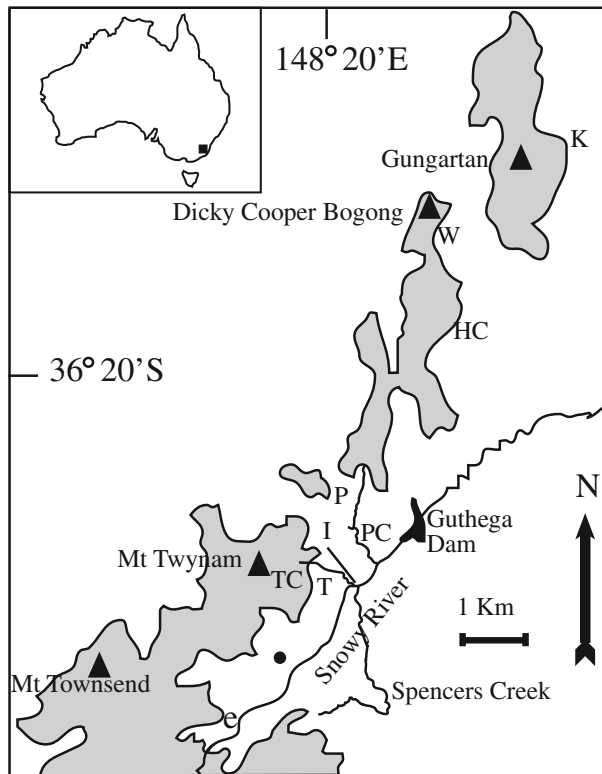


FIGURE 1. Map of the study area showing the location of the study tree-limit ribbons and the area above 1900 m (shaded). Ribbons were T = Twynam (unburnt), I = Illawong (2 ribbons, one unburnt), P = Pounds Creek (unburnt), HC = Horse Camp (3 ribbons, one unburnt), W = Whites River (burnt), and K = Kerries (unburnt). The transect through five parallel ribbons begins at ribbon I; TC = Twynam Creek, PC = Pounds Creek and its northeasterly extension, e is the location of the two establishment-phase ribbons. The filled circle is the location of the seed-bearing snowgum branch.

trees above, were chosen. Ribbons with adjacent substrates not conducive to seedlings growth, i.e. consisting predominantly of rock or wetland, were excluded. Three classes of ribbons were examined: unburnt ($n = 5$), burnt (in 2003 wildfire; $n = 4$), and early establishment-phase unburnt ribbon ($n = 2$) (Fig. 1).

To examine the dynamics of tree establishment downslope of a tree ribbon, a transect was established in a burnt area below one of the unburnt ribbons (Fig. 1). On this long slope, five parallel ribbons occurred at intervals down to the general level of the frost hollow at the confluence of the Snowy River and Spencers Creek. Here, the largest tree stems and lignotubers (basal meristematic swellings) in each ribbon encountered on the slope were measured, and the location of seedlings, krummholz, shrubs, and grasses were recorded. This area was chosen, as there was no possibility of the trees establishing uphill from the river flats where trees were absent, and hence the initial colonization must have been from a distance involving windblown propagules. In addition, all the trees in an area of approximately 3 km², bounded by the Snowy River, Twynam Creek, and Pounds Creek and its northeasterly tributary (Fig. 1), were assessed to determine their stem age relative to the oldest trees in the highest ribbons. This included trees in un-surveyed tree ribbons (uncounted), individual trees and those in non-linear clumps (total >850 trees).

PHYSICAL ATTRIBUTES

At each site, we marked the plots for permanent monitoring, recorded altitude, the orientation of the ribbon and the aspect of the slope (using GPS and compass), as well as slope through the ribbon and the slope beneath the ribbon (using a clinometer).

To determine how tree ribbons affect local wind speed, we measured wind speed between February and April 2010 (during the snow-free season) at each ribbon in paired comparisons using two identical and calibrated Kestrel 1000 anemometers with attached vane mounts (Nielsen-Kellerman, Boothwyn, Pennsylvania). These were mounted on tripods of the same height (approximately 60 cm) above the ground, in grassy areas free of tall shrubs, just outside the canopy area upwind and approximately 10 m downwind of the ribbon out of the canopy zone. The paired anemometers were run for a minimum of 10 min at each sampling time and the average wind speeds for that period were compared using paired *t*-tests.

To determine whether soil properties within tree ribbons differed from areas above and below, we measured soil depth at three locations in each of three zones: above, within, and below each ribbon, by inserting a steel probe until it hit impassable rock. Mea-

TABLE 1

Characteristics of snowgums within the study ribbons and physical/topographic data. UB = unburnt, B = burnt. Tree heights and stem ages could not be assessed accurately in burnt ribbons.

	Burnt or unburnt	Ribbon length (m)	Ribbon width (m)	Tree Height \pm 1SD (m)	Tree stem age (yr) (max)	Tree stem age (yr) (mean)	Altitude (m)	Slope orientation $^{\circ}$ true	Slope angle% in ribbon	Slope angle% below ribbon
Twynam	UB	68	18.5	9.1 \pm 2.1	223	148	1840	110	12	16
Illawong	UB	143	27	6.3 \pm 1.1	496	182	1835	140	7	17
Illawong	B	216	14.7	N/A	N/A	N/A	1845	55	10.5	15
Pounds Creek	UB	194	25	6.9 \pm 1.5	323	158	1785	90	0.5	18
Horse Camp	UB	132	28	8.6 \pm 2.6	305	154	1805	70	5	15
Horse Camp 1	B	304	17.5	N/A	N/A	N/A	1846	105	6	11
Horse Camp 2	B	200	30	N/A	N/A	N/A	1848	86	10.5	18.5
Whites	B	189	31	N/A	N/A	N/A	1875	89	6	13
Kerries	UB	103	21.5	6.8 \pm 1.7	184	120	1910	75	8	20

measurements were taken to a maximum depth of 60 cm (thereafter recorded as >60 cm if rock had not been encountered). Three soil samples were collected from above, within, and below each ribbon to a depth of 10 cm and bulked. Chemical soil analyses for 21 attributes (nutrients and other elements) were conducted at the CSBP Soil & Plant Laboratory (CSBP Limited, Bibra Lake, West Australia). Analyses conducted were for ammonium, nitrate, phosphorus, potassium, sulfur, organic carbon, conductivity, pH, copper, iron, manganese, zinc, aluminum, calcium, magnesium, sodium, boron, and organic matter. One way ANOVA was used to test for significant differences in each attribute above, within, and below the ribbons, treating each attribute separately and pooling across ribbon sites. Before analysis, values were standardized by means and standard deviations; site mean (mean of above, below, and within ribbon) subtracted from each of the above, within, and below values, then divided by the site standard deviation to isolate variation within sites and therefore test for deviations from mean nutrient/mineral values that relate to position in and around the ribbons, without the confounding effects of between-site differences. Soil moisture (%) was measured five times above, within and below each ribbon using a ThetaProbe soil moisture sensor type ML2x and HH2 reader (Delta-T Devices, Cambridge, England) for the purpose of comparison within each ribbon only, as moisture measurements could not be made on every ribbon on the same day. Differences in soil moisture were compared using paired *t*-tests.

To determine whether tree ribbons affect the depth and duration of snow cover, snow depth was measured in winter 2010 from the center point of each ribbon and subsequently every 2 m above and below the ribbon to a distance of 50 m using a 3.2 m avalanche probe. A Tinytag Plus temperature logger (Gemini Data Loggers, Chichester, England) recording at 60 min intervals was buried beneath approximately 10 cm of soil, above and below each ribbon over the winter of 2010 in order to determine the commencement of the snow-free season at the end of winter. This point was determined from the beginning of fluctuation in the temperature trace, indicating melting snow. Within this period of fluctuation, the actual day of thaw was determined as the date when the temperature first rose above 3.2 °C at noon or within 2 hours either side of noon; this day was also taken as the commencement of the growing season (Körner and Paulsen, 2004; Green and Pickering, 2009b).

TREE DATA

At each fully established ribbon, width and length of the ribbon were recorded. At unburnt ribbons, the heights of five trees representative of the general canopy were measured using a clinometer and rangefinder and then calculated using trigonometry.

To estimate the general age of the trees that constituted the ribbons, the maximum diameter across the largest lignotuber and the girth of the largest live stem originating from that lignotuber, were measured on trees every 3–4 m along the length of each ribbon.

To determine the distribution of trees, saplings, and seedlings outside of the ribbons, we established belt transects 30 m in width upslope and downslope of each ribbon, extending approximately 50 m perpendicular to the ribbon. The center point of each belt transect intersected with the approximate center of the ribbon (also the point where ribbon width was measured) and hence never en-

compassed either end of the ribbon. Within the belt transects, the distance of each seedling, sapling, or tree from the ribbon edge, whether above or below the ribbon, its height, and main stem girth were recorded. Stem girth was measured immediately above the basal swelling of the lignotuber to calculate stem age. Diameter was measured instead of girth in cases where the stem was growing along the ground.

At burnt ribbon sites, the status (either burnt or unburnt) of all seedlings, saplings, and trees was recorded. The largest stems that had burnt through completely were recorded and the diameter at the point where stems burnt through was measured for between 5 and 10 stems in each of the burnt transects. This measurement was used to determine the minimum size (and hence stem age) of burnt remains expected above ground.

The ages of living stems were estimated from basal girth based on two previous studies of growth-ring–basal-girth relationships (Barker, 1988; Rumpff et al., 2009). *Eucalyptus pauciflora* at high altitude exhibit seasonal growth with annual growth rings and few false or missing rings (Banks, 1982; Brookhouse et al., 2008). Seedlings and saplings found in the belt transects were estimated from basal girth using $y = 3.62x^{0.63}$, $R^2 = 0.96$ which is derived from treeline trees of girth less than 115 cm (Rumpff et al., 2009) and the formula $y = 1.20x + 0.0$, $R^2 = 0.93$ for basal girth age of larger trees within the ribbons based on measurements of trees at 100 m below treeline (Barker, 1988).

Windblown branches from snowgum, and other eucalypt species, are frequently seen above the treeline, particularly on winter snow (K. Green, personal observation). To determine whether viable seed could be spread uphill in this manner, seed capsules were collected from a freshly detached branch (1.5 m long) found at 1850 m above a frost hollow and 1.5 km downwind of the nearest snowgum (Fig. 1). From these capsules, 30 filled seeds were tested for viability (3 groups of 10) using standard tetrazolium staining (Moore, 1985).

Results

RIBBONS

The study ribbons lay at altitudes of 1785–1910 m. All studied tree ribbons were on slopes with aspect in an arc of less than 90°, varying from northeast to southeast (55° to 140°). The slope angle through the width of the ribbons varied between 0.5% and 12% but steepened immediately below the ribbons to 11–18.5%. Mean slope below the ribbon was twice that within the ribbon (14.6% compared with 7.3%; $n = 9$, $t = 7.57$, $p < 0.0001$).

PHYSICAL ATTRIBUTES

Mean wind speeds upwind (uphill) of ribbons were 2.15 times the downwind (downhill) speed ($t = 3.91$, $p = 0.005$). There was no significant difference between the degree of wind reduction downwind of burnt or unburnt ribbons.

There were no significant differences among soil depths above (37.9 ± 6.6 cm), within (34.1 ± 11.6 cm), or below (34.7 ± 8.7 cm) the ribbons. There were also few significant differences in chemical soil attributes from above, within, and below the ribbons

TABLE 2

Mean (± 1 standard error) of chemical soil attributes (nutrients, trace elements, minerals, and extractable ions) in soils immediately above, within, and below ribbons. Key: NH₄, NO₃, P, K, S: (mg kg⁻¹); OC: organic carbon content (%); COND: conductivity (dS m mg⁻¹); pH (Ca), pH (H₂O): soil pH analyzed with calcium, water; Cu, Fe, Mn, Zn: (mg kg⁻¹) extracted using diethylenetriaminepentaacetic acid (DPTA); extractable ions of Al, Ca, Mg, K*, Na: (meq/100 g); K* is extractable K; Al (CaCl₂), Bo (CaCl₂): aluminum and boron extracted using calcium chloride (mg kg⁻¹); OM: organic matter content (%).

Attribute	Above ribbon	In ribbon	Below ribbon
NH ₄	33.9 \pm 7.8	30.3 \pm 6.86	18.4 \pm 3.16
NO ₃	27.8 \pm 9.32	8.37 \pm 2.26	19.8 \pm 4.95
P	32.9 \pm 3.23	49.38 \pm 8.98	52.6 \pm 6.46
K	234.37 \pm 16.21	260.3 \pm 18.7	257 \pm 27.5
S	7.9 \pm 0.74	7.67 \pm 1.19	6.64 \pm 0.56
OC	8.83 \pm 0.62	9.52 \pm 0.27	9.31 \pm 0.23
COND	0.08 \pm 0.014	0.6 \pm 0.01	0.07 \pm 0.01
pH (Ca)	1.38 \pm 0.02	1.34 \pm 0.03	1.38 \pm 0.02
pH (H ₂ O)	1.55 \pm 0.02	1.53 \pm 0.02	1.55 \pm 0.02
Cu	0.48 \pm 0.05	0.43 \pm 0.03	0.64 \pm 0.09
Fe	169.97 \pm 11.67	221.1 \pm 15.9	156 \pm 10.7
Mn	5.108 \pm 1.27	4.58 \pm 0.91	9.94 \pm 2.87
Zn	0.9 \pm 0.13	0.93 \pm 0.11	1.24 \pm 0.26
Al	6.76 \pm 1.08	8.28 \pm 1.03	6.35 \pm 0.61
Ca	2.31 \pm 0.62	1.73 \pm 0.42	2.06 \pm 0.51
Mg	0.83 \pm 0.11	0.88 \pm 0.15	0.69 \pm 0.14
K*	0.60 \pm 0.04	0.65 \pm 0.04	0.63 \pm 0.07
Na	0.07 \pm 0.018	0.06 \pm 0.01	0.05 \pm 0.01
Al (CaCl ₂)	39.69 \pm 9.99	52.47 \pm 11.4	35.7 \pm 5.43
Bo (CaCl ₂)	0.712 \pm 0.05	0.08 \pm 0.11	0.84 \pm 0.11
OM	16.67 \pm 2.44	21.64 \pm 2.36	19.4 \pm 1.31

and no overall trends among the ribbons (Table 2). However, there were some significant differences across the ribbons in particular attributes; nitrate levels were significantly lower within ribbons than above and below ($df = 2$, $F = 3.67$, $p = 0.043$), phosphorus levels below ribbons were significantly higher than above ($df = 2$, $F = 5.44$, $p = 0.012$), copper levels below ribbons were significantly higher than within ribbons ($df = 2$, $F = 4.23$, $p = 0.029$), iron levels in ribbons were significantly higher than above and below ($df = 2$, $F = 16.79$, $p < 0.001$), and sodium levels below ribbons were significantly lower than above ($df = 2$, $F = 5.503$, $p = 0.012$). There was no significant difference between soil moisture upslope of ribbons compared to within ribbons ($t = 1.333$, $p = 0.212$), but soil moisture within ribbons was significantly higher than downslope of ribbons ($t = 3.438$, $p < 0.05$).

Maximum snow depth was highest downwind of the ribbons in all cases except Illawong Burnt (Table 3). Snow depths downslope of ribbons ranged between 107% and 309% of the depth of snow within ribbons and between 84% and 480% the depth of snow upslope of ribbons. Snow depth was also greater upwind of ribbons than within the ribbons but not significantly so. Three of the four deepest snow drifts were downwind of unburnt ribbons and the two shallowest snowdrifts were downwind of burnt ribbons (Table 3).

Mean (± 1 sd) snowmelt date upwind of the ribbons was significantly earlier than downwind of ribbons (Julian day 279 \pm 10

TABLE 3

Maximum snow depths (cm) above, within, and below ribbons. UB = unburnt, B = burnt.

Ribbon	Above ribbon	In ribbon	Below ribbon
Twynam	204	110	340
Illawong UB	223	179	>380
Illawong B	172	135	145
Pounds Creek	180	183	309
Horse Camp	190	113	235
Horse Camp B1	121	121	134
Horse Camp B2	122	100	293
Whites	75	122	>360
Kerries	225	240	>360

upwind, compared with day 301 \pm 14 downwind, $t = 4.19$, $p = 0.003$). There was no significant difference in snowmelt date between burnt and unburnt ribbons.

TREE DATA

Burnt and unburnt ribbon lengths ranged from 68 to 304 m, and between 15 and 31 m in width (Table 1). Mean tree heights measured from five representative trees within each ribbon ranged between 6 and 9 m (Table 1). Overall, the range of maximum and mean ages of stems from the largest trees every 3–4 m along the length of each ribbon were between 184–496 and 120–182 years, respectively (Table 1). Tree stems were younger at the ends of ribbons than in the center. Lignotuber sizes (which were generally older than the existing stems), also showed a strong decline in size towards the ends. However, this reduction in age/size was not evident across the ribbon, from upslope to downslope, with the oldest trees and/or largest lignotubers frequently being on the uphill or downhill edge. This pattern was also evident in the two 'establishment-phase' ribbons. The first, oriented 122°, had only six trees with two, 2.8 m apart, aged 150 and 151 years at one end, with younger trees occurring laterally. The second establishment-phase ribbon was oriented 89° with the two oldest trees (and largest lignotubers) located centrally, with younger trees spread laterally across the slope (Fig. 2).

In the transect established to examine the dynamics of tree establishment, downslope of the Illawong study ribbon (Fig. 1), shrubs, seedlings, and krummholz existed immediately below the ribbons (Fig. 3). Patches of grass occurred where snowdrifts accumulated in winter and in a small frost hollow above the lowest ribbon. The area below the Illawong study ribbon was burnt in 2003 and hence accurate ages of the intervening emerging young snowgums could not be determined, although most appeared to predate the fire and have since resprouted from lignotubers. The age of the oldest stems in these ribbons declined from 496 years at the highest ribbon to 378 years at the lowest. Lignotuber size also declined down the transect (Fig. 3); the largest lignotuber was found at the highest ribbon, and lignotuber size generally declined with subsequent ribbons downhill, with the exception of ribbon 4 (at the bottom of the initial hill) which had the second-largest lignotuber. On the same slope, but within the boundary of the

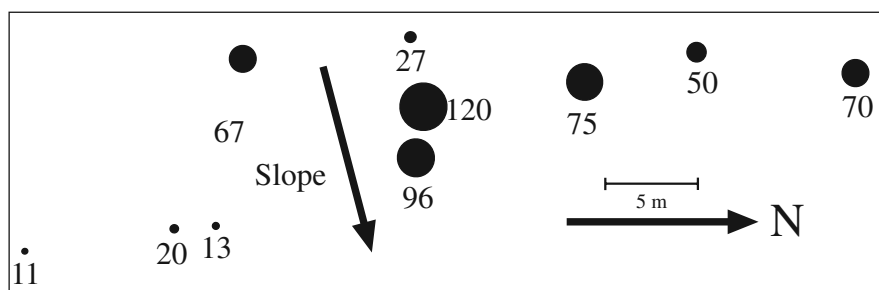


FIGURE 2. The arrangement of trees (filled circles) within an establishment-phase tree-limit ribbon and their calculated stem age; the scale is only for distance, tree girths are exaggerated but are correct relative to one another.

Snowy River, Twynam Creek, and Pounds Creek, girth measurements indicated that all tree stems in the area were younger than the stems in the highest ribbons.

Mean counts of snowgum seedlings, saplings, and trees in belt transects were significantly higher downslope of each ribbon than upslope (0.8 above and 14.3 below; $t = 3.43, p = 0.009$). Overall, 128 snowgums were found in the transects downslope of the ribbons compared with 7 upslope. Downslope of the ribbons, 51.6% of seedlings/saplings were found within 10 m of the edge of the ribbon, 35.2% in the next 10 m, with 9.4%, 2.3%, and 1.6% in succeeding 10 m intervals. Downslope of unburnt ribbons, 48 snowgums were found with 80 snowgums found downslope of burnt ribbons.

The maximum diameter of stems burnt completely through in belt transects was 23.5 mm (about 13 years); therefore, snowgums with no above-ground (burnt) remains had either established in the 13 years pre-fire and resprouted from lignotubers or had established post-fire. This made their age <22 years and hence, although they could not be plotted by decade, they had established in the period post-1970. Most trees in the burnt plots did not actually burn and could therefore be aged. Estimated mean (± 1 sd) of unburnt stem age downslope of ribbons was 19.4 ± 13.7 , with 88% of trees being less than 40 years of age (Fig. 4).

Tetrazolium staining and interpretation revealed that the three groups of filled seeds collected from the windblown branch above treeline were highly viable (50%, 77%, 87%).

Discussion

TREE RIBBON CHARACTERISTICS AND FORMATION

Tree-limit ribbons have previously been described only in North America (Buckner, 1977; Holtmeier, 2003; Bekker and Malanson, 2009). We are the first to identify them in Australia and for broadleaf evergreen species. Type 1 ribbon forest (Buckner, 1977), those isolated ribbons of trees growing perpendicular to prevailing winds at close to tree limit as in this study, have not been well studied (Bekker et al., 2009). Elsewhere, linear tree features occur as hedges, extensive ribbon forest, ridge-top ribbon forest, and waves (Billings, 1969; Bekker and Malanson, 2009). Tree-limit ribbons in the Snowy Mountains are all on lee slopes and are established well above the current treeline. The abrupt edges of ribbons dominated by old trees (with only recent establishment outside of these edges), as observed in this study, indicate that these ribbons have been stable over many hundreds of years, as found in tree-limit ribbons in North America (Buckner, 1977; Holtmeier, 2003).

The causes of tree ribbon development may be site-specific (Bekker et al., 2009). Here, the significant difference between the slope angle within and downslope of the study ribbons suggests that slope topography is important. Microtopography associated with intrusive bedrock or solifluction terraces was implicated in ribbon formation in North America; this was associated with shelter and snow accumulation and protection from gophers (*Thomomys talpoides*) (Buckner, 1977; Holtmeier, 2003). Only one native her-

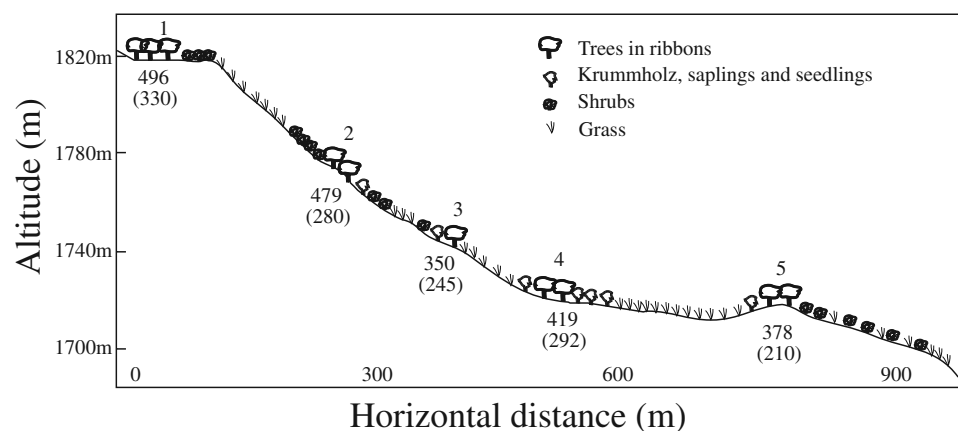


FIGURE 3. Profile view of parallel ribbons from the Illawong tree-limit ribbon (1) downhill to a frost hollow at the Snowy River. Figures below ribbons are the maximum calculated age for a tree stem in that ribbon and figures in parentheses are maximum lignotuber diameter (cm).

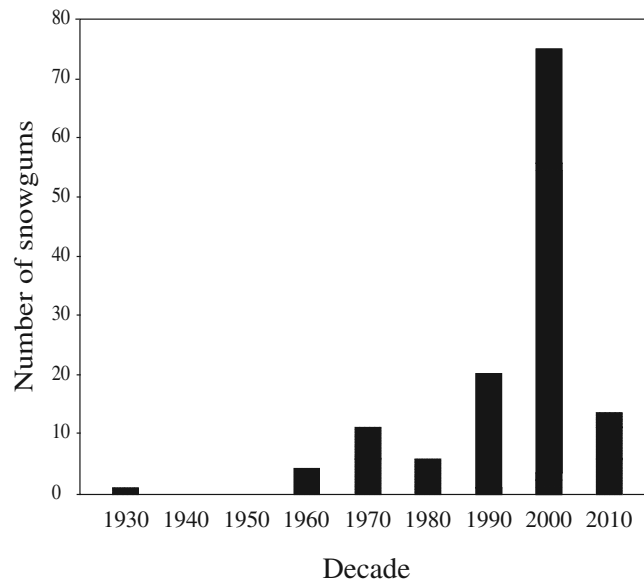


FIGURE 4. The age distribution of 130 seedlings and saplings below tree-limit ribbons by decade. Vertical bars indicate the number of snowgums along belt transects for the 10 years up to the date given.

bivorous mammal, the broad-toothed rat (*Mastacomys fuscus*), occurs in the alpine/treeline zone of the Snowy Mountains (Green and Osborne, 1994) and it does not damage tree seedlings. Whilst the accumulation of snow, intermediate between too little for protection of seedlings in winter and too much to allow an adequate growing season post-thaw, may occur on the edge of terraces, the effects of the current presence of trees makes it difficult to determine conditions before their establishment. Steps above rises may favor tree growth because of higher ablation and warmer soil, associated with increased solar radiation striking a flat surface embedded in a steep south-facing slope, providing earlier snow-free ground for seedling establishment and warmer conditions for subsequent growth.

Once trees are established, lateral spread of the ribbon does not appear to be by the coalescence of tree clumps as suggested in the Medicine Bow Mountains (Earle, 1993), because here the oldest snowgums were located in the center of the ribbon. Neither does lateral spread occur through vegetative growth (Billings, 1969). Layering, formation of adventitious roots, leading to clonal groups of trees, occurs more frequently at higher elevation and is the rule rather than the exception at treeline in the Rocky Mountains where *Abies lasiocarpa* and *Picea engelmannii* form ribbons (Holtmeier, 2003). However, although vegetative reproduction is more common in broad-leaved trees than in conifers (Holtmeier, 2003), *E. pauciflora* can only regenerate and spread through seed. Although *E. pauciflora* can resprout from lignotubers after fire or frost damage, this is regrowth of a single tree rather than clonal spreading and therefore does not contribute to lateral spread across the slope. In the present study, there is no convincing evidence that differences in geology or soil may promote the linear spread of trees across slopes. Whilst most sites had large intrusive rocks that may trap windblown branches in winter and facilitate initial snowgum establishment through warmth and protection from wind, these were not spread the length of the ribbons and were also present outside of tree ribbons, so were probably not associated with subsequent lateral spread. Soil depth was similar above, within, and below ribbons and although nutrient levels varied across the ribbons, there is no evidence that boundaries of *E. pauciflora* woodlands are associated with soil nutrient status (Moore, 1959). Furthermore, differences in soil nutrients under *E. pauciflora* woodland compared to nearby grassland appear to be due to the influences of the trees on the soil rather than any pre-existing differences between soils before colonization by trees (Hedenstroem, 1993). We found some differences in soil chemical attributes between soils within ribbons and in the open, however, the fact that the differences in Ca, Mn, Al, N, and P were generally the reverse of those found by Hedenstroem (1993) suggests that soil nutrients within a ribbon are not preferentially limiting or facilitating growth. As with conditions on solifluction terraces on the Niwot Ridge (Colorado Front Range) (Daly and Shankman, 1985), sites on the



FIGURE 5. Parallel tree-limit ribbons on the south-east flanks of Mt. Twynam, Snowy Mountains, Australia.

steps above rises were wetter than on the steeper slopes below. However, ongoing tree establishment downslope of ribbons suggests that neither soil nutrient status nor soil moisture are important determinants of seedling establishment at ribbons in the Snowy Mountains.

The establishment of snowgums uphill of the current treeline suggests physical movement of more than just the seed, for example, tree branches being blown uphill in storms (Green, 2009). Although we found highly viable seed from windblown branch-borne capsules collected above treeline, rates of successful germination of snowgum seed and subsequent seedling establishment at treeline under natural conditions are notably low. Reported germination rates for seed sown at or above the treeline in the Snowy Mountains for example, are less than 6% (Ferrar et al. 1988; S. Venn, unpublished). Despite such low germination, seedlings have established at sites much higher than the treeline (Slatyer, 1989). Once the initial threshold of germination and seedling establishment at alpine treeline is attained, survival of *E. pauciflora* subsp. *niphophila* is relatively high, with 77% of seedlings planted above treeline under natural conditions alive after one year (K. Green, unpublished).

ENVIRONMENTAL FACTORS AFFECTING TREE-LIMIT RIBBON DYNAMICS: PAST AND PRESENT

Once established on the broad lee slopes that characterize the Snowy Mountains, snowgums have spread along the contour, forming ribbons. This chronology can be inferred from the distribution of tree sizes (and apparent age) along the unburnt studied ribbons and the establishment-phase ribbons with a probable spread from a central tree or group of trees laterally across lee slopes with little successful colonization upslope or downslope. As expected, these ribbons do reduce wind; upwind of ribbons average wind speed was 2.15 times that of the downwind speed. In the Medicine Bow Mountains (U.S.A.), average wind over a one-month period at a similar height above ground (65 cm) was 19 times higher in the open than in ribbons (Billings, 1969). Such ribbons are thought to act in the manner of a snow fence, collecting snow immediately downwind where the snow cover is too prolonged to allow seedling establishment (Billings, 1969). At our study ribbons over the 2010 season, there was a mean difference of three weeks in the thaw date between the tree ribbons and their immediate downwind area, and hence the length of the growing season. The dominant mechanism for snowdrift interception downwind of tree ribbons may be exogenous, with microtopographic relief being more important than the ribbons, although there is also an appreciable endogenous effect, because on north-facing slopes, snowdrifts still occur down-wind but upslope of ribbons (K. Green, personal observation).

The ability of trees to slow wind, as well as contribute to the accumulation of snow drifts, is a function of the distance from the windbreak (Geiger, 1975). Downwind of a deciduous windbreak of trees on parallel dikes in South Dakota, snow depth was not affected beyond about 35 m (Vose and Dunlap, 1968), a similar distance to that in the Snowy Mountains. Successful establishment of trees (as distinct from krummholz) downwind of ribbons in the Snowy Mountains was achieved only where snow depth was reduced to normal snowpack depth.

In the past 40 years, there has been a pulse of establishment downslope of tree ribbons by seedlings. About 87% of seedlings/saplings downhill of the ribbons were found within 20 m of the edge, where they generally occurred in the cover of the snowdrift. The ratio of snowgums below to above ribbons (within 15 m of the edge) of 13:1 was similar to the 17:1 found at the treeline by Green (2009). Changes in snowdrift patterns do occur post-fire (Billings, 1969) and here only one of the four deepest snow drifts and the two shallowest snowdrifts were below burnt ribbons. Fire can damage the outer layers of snowgum stems, similar in effect to ringbarking, causing canopy losses (Wimbush and Costin, 1979). Structurally, burnt snowgum ribbons therefore act the same as a windbreak of deciduous trees that have only about 60% of the impact in winter as in summer (Geiger, 1975). However, fire does not appear to be an important factor in the process of seedling establishment as most stems in burnt sites resprouted from stock present before the 2003 fire.

Allowing for some error in ageing of stems, nearly 90% of snowgums downwind of ribbons appear to have established since 1970. Since no fire or other major disturbance such as grazing immediately precedes this period (as evidenced by 200-year-old stems along the length of ribbons), the current spread of seedlings from the ribbons is likely to represent natural growth after a long period of absence of trees from the site. Alternatively there may be high periodic mortality of seedlings, which would tend to show as large but temporary populations (Daly and Shankman, 1985). This period, post-1970, coincided with regional warming and drought (BOM, 2011). A similar timing of a pulse of seedling establishment in the Southern Rocky Mountains was documented by Elliott and Kipfmüller (2010) with synchronous growth of 64% of trees establishing above timberline since 1970 and 91% since 1950. The low level of establishment from 1950 to 1970 in the Snowy Mountains may reflect the fact that 4 of the 10 heaviest snow years on record occurred in the period 1960–1970. This may have delayed vegetative responses to reduction in snow, despite observed temperature increases, or it may have killed seedlings due to ice abrasion or mortality due to fungal attack beneath snow (Holtmeier, 2003).

The results indicate that a breakdown of the wind-fence effect due to a lack of an inhibiting, long-lasting presence of snow may be sufficient to allow establishment of seedlings. Snow near treeline therefore appears to play two contrasting roles: by an extended seasonal presence, it facilitates seedling growth by protection against winter conditions up to a point; beyond that point it reduces the length of the growing season sufficiently to suppress growth (Bekker, 2005; Elliott and Kipfmüller, 2010). There is a fine line between these contrasting functions, because trees near treeline are already at their physiological limit and even the slightest reduction in growing season may be sufficient to suppress growth. Conditions at the current treeline of the Snowy Mountains are unlikely to represent the conditions under which those treelines developed. Owing to regional warming, treeline temperature measurements today (Körner, 2003; Körner and Paulsen, 2004) are perhaps 0.6 °C higher than those when treeline establishment occurred. This means that trees establishing up to 100 m above existing treelines may currently be within their physiological tolerances. Since 1970, spring warming and a reduction in the amount of snow during drought have led to an earlier thaw and hence a longer growing

season. Together with increased warmth within the growing season, these factors may have acted together to tip the balance in favor of promoting seedling establishment and growth.

The transect through five ribbons on the lower flanks of Mt. Twynam (Fig. 3) gives an indication of how ribbon forest elsewhere in this region might have established in the past. Leaving aside the possibility of five independent establishments at different altitudes up the slope, the presence of the oldest tree stem and the largest lignotubers suggests that initial establishment occurred at the highest ribbon. Seeds must have dispersed from afar because the frost hollow downslope in the Snowy River valley does not support trees. Natural seed dispersal by gravity and subsequent seedling establishment could only have been downhill beyond the snowdrift zone below the highest ribbon and so on down the slope, with possible leapfrogging to the bottom of the slope. This contrasts with the view of Buckner (1977), Earle (1993), and Holtmeier (2003) that snowdrifts do not encourage the downwind establishment of ribbons. However, the mechanism here is not as suggested by Billings (1969), but simply the facilitation of movement of seed downhill. As with the spread across slope from a founding tree or trees, genetic studies may be necessary to track the provenance of trees in these ribbons at descending altitudes. Again, as with the isolated ribbons studied here, these would have been stable for some time until some climatic factor such as drought, with reduction in the snow season, allowed new establishment, which has been prolific in some areas of the transect. In this way, infilling between the ribbons might allow the establishment of contiguous subalpine woodland below a new treeline. Elsewhere on the same slope, over 850 trees, all younger than those uphill in the tree ribbons, have established as either individuals or clumps, also adding to the infilling between the ribbons and the treeline. Infilling between ribbons and the existing treeline, either by intervening ribbons or by scattered or otherwise-clumped trees, may be the fastest mechanism by which the contiguous subalpine woodland can respond to a changing climate and advance to a new elevation.

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