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Lachnagrostis (Poaceae) in the Highlands of New Guinea

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Abstract

The Australian grass, *Lachnagrostis aemula* (R.Br.) Trin. is identified among numerous collections of *L. filiformis* (G.Forst.) Trin. from Papua New Guinea and Western New Guinea. Both species are confined to sub-alpine grasslands at elevations of 1700–3700 m, where rainfall and humidity are high and temperatures are relatively low and uniform throughout the year. While *L. filiformis* is most commonly found on human-disturbed sites, *L. aemula* appears to be associated with more natural sites: a similar habitat preference to that found in Australia.

Keywords: Blown-grass, Papua, Irian Jaya, Biogeography

Introduction

Botanical exploration of the Highlands of New Guinea began in the early part of the 20th century. Among the many plants collected from this region were numerous specimens of the C3 grasses, *Lachnagrostis* Trin. and *Agrostis* L. A cursory examination of the *Lachnagrostis* collections suggest that more than one taxon is present. This paper investigates these specimens in more detail and considers their relationship to Australian *Lachnagrostis* taxa in terms of morphology and habitat.

Physiography and vegetation of the New Guinea highlands

The Island of New Guinea (NG) comprises of the nation of Papua New Guinea (PNG) on the eastern half (formerly British New Guinea in the south and German New Guinea in the north) and the Indonesian provinces of West Papua and Papua which make up Western New Guinea (WNG) or Irian Jaya (formerly Dutch or Netherlands New Guinea) on the western half. The NG Highlands are a central chain of mountains running the whole length of the island from west to east, of which the highest peaks are Puncak Jaya (Carstensz Pyramid, Mt Carstensz, Mt Jayawijaya), WNG (4884 m alt.); Puncak Madala (Juliana-top, Juliana Peak), WNG (4760 m alt.); Puncak Trikora (Wilhelmina-top, Mt Wilhelmina), WNG (4750 m alt.); Mount Wilhelm, PNG (4509 m alt.), Mt Giluwe, PNG (4368 m alt.) and Mt Victoria, PNG (4038 m alt.). The tree line occurs at about 4000 m and the highest peaks contain permanent glaciers. Montane forests (*Castanopsis*, *Nothofagus*, Coniferous), lower montane grasslands and

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swamps (*Miscanthus–Imperata*, *Phragmites*, *Machaerina*) and Tree-fern savanna (*Cyathea*) occupy much of the Lower Montane Zone with altitudes from 1000–3000 m on long slopes, spurs and ridges (Paijmans 1976). Most of the lower montane grasslands and sedge swamps are likely the result of land clearing and deliberate firing for agricultural purposes. Above 3000 m, the Upper Montane Zone is comprised of discontinuous ridges, peaks and plateaus with plant communities of forests (Myrsinaceae, Ericaceae, Myrtaceae, Rubiaceae, Conifers), sub-alpine grasslands (incl. *Deschampsia* P.Beauv., *Monostachya* Merr., *Poa* L., *Festuca* L. and *Danthonia* DC spp.) and herbaceous swamps (incl. *Anthoxanthum* L., *Agrostis* L., *Carpha* Banks & Sol. ex R.Br., *Gleichenia* Sm., *Astelia* Banks & Sol. ex R.Br., *Leucopogon* R.Br. and *Drapetes* Banks ex Lam. spp.) (Paijmans 1976).

Climate of the New Guinea highlands

Day-time temperatures in the Highlands show little variation throughout the year but decrease as altitude increases. Mean annual temperature across the Highlands is 19°C at 1500 m, 17°C at 2000 m, 14°C at 2500 m, 12°C at 3000 m and 10°C at 3500 m (McAlpine et al. 1983). Night temperatures are usually about 10°C lower than day temperatures. Rainfall, although relatively high across the island, tends to decrease from the west to the east. At Puncak Jaya, annual rainfall is 5500 mm, while at Mt Hagen in the Western Highlands Division of PNG, annual rainfall is 2577 mm with a range from 129 mm in June and 294 mm in March. In contrast, the Lowlands of NG have a maximum temperature of 30–32°C and minimum of 23–24°C (diurnal and seasonal variation being similar). The tropical Lowlands experience a more pronounced monsoonal season than the Highlands, with a definite dry season. The direction of trade winds and the influence of mountain ranges in producing rain shadows, result in widely ranging annual rainfall from less than 1000 mm to 2200 mm. Humidity in the Lowlands is uniformly high at 80%, while it varies from 65% to 80% in the Highlands.

Plant collecting in the New Guinea highlands

Although a few exploratory treks to the highest peaks in both PNG and WNG were made from 1906, it wasn't until the 1920's that a few European gold seekers started pushing into the interior, following rivers from the coast. The Morobe gold field near Wau (1100 m alt.) was the site of limited gold mining during 1924–1926 but it was at the Upper Edie Creek, 5 km away, that a gold rush began in 1926 (Waiko 1993). The earliest European contact with the people of the Highlands was in the 1930's, by the Queenslander Mike Leahy and his brothers in search of gold. The Highlands were found to be densely populated, and its peoples engaged in complex systems of agriculture (e.g. clearing, burning, fallow, crop rotation), landscape gardening (e.g. drainage, mounding, terracing, irrigation, fencing) and silviculture (Bourke 2009). Most people live and farm in broad valleys between 1500 m and 2000 m (Brown 1978, McAlpine et al. 1983), where high plant productivity is ideal due to rainfall being adequate but not excessive, soil moisture is abundant, soils are fertile, diurnal temperature changes are relatively large and frosts are rare (Bourke 2017). Food production altitudinal zones for NG have been defined as lowlands: sea level to 600 m; intermediate: 600–1200 m; highlands: 1200–1800 m; high altitude 1800–2400 m; very high altitude: 2400–2800 m; uninhabited: > 2800 m (Bourke 2017).

The earliest biological collections from the mountains of WNG were those of the first Dutch South New Guinea Expedition of 1907–1908, led by Hendrikus Albertus Lorentz, which reached the Hellwig Mountains (2320 m alt.) (Marshall & Beehler 2011). The second Expedition of 1909–1910, again led by Lorentz, and the third of 1912–1913, led by Franssen Herderschee, made their way into the Snow Mountains and eventually to Puncak Trikora. Also in 1912–1913, F.R. Wolleston leading a British Expedition, with the assistance of C. Boden Kloss (Kuala Lumpur), to the WNG Highlands, reached Puncak Jaya. The Central New Guinea Dutch Expedition of 1921–1922 and 1922–1923, led by A.J.A. Overeem and J.H.G. Kremer, respectively, explored the Swart (Toli) Valley and Doorman Mountains (2750–3500 m alt.).

Botanical exploration of the PNG Highlands began in earnest with the Archbold Expeditions from 1833 to 1839 and again from 1853 to 1964. Richard Archbold was a self-funded, private explorer who financed seven expeditions to PNG and WNG, with Queenslander, Leonard John Brass as the principal botanist. Of these, the first (1933–1934), third (1938–1939) and seventh (1964–1965) included exploration of montane forests, subalpine and alpine environments. Since the 1950's, continuous plant collecting from the Highlands has occurred, particularly in association with agricultural and forestry development, administrative postings and general plant surveys by botanists, both from within PNG and without (particularly Australia) (Frodin 1990).

Materials and Methods

A review of *Lachnagrostis* and *Agrostis* collections made in NG (WNG & PNG) was made through the Netherlands Biodiversity API (BioPortal 2018) of the Naturalis Biodiversity Center (NHN: L, U, WAG), the Australasian Virtual Herbarium (AVH 2018) (Australia and New Zealand herbaria) and the Plants of Papua New Guinea (PNGplants 2018) (LAE, BRI, CANB, NSW, MEL) websites.

Collections of *Lachnagrostis* from NG, lodged at L, BRI and CANB, were examined and morphological measurements made for various vegetative, inflorescence and spikelet characters (Table 1) on a range (29) of specimens (App. 1). The characters measured represent those often used in descriptions and diagnostic keys used for these grasses (Jacobs & Brown 2009; VicFlora 2018) and the specimens examined were assessed in accordance with those descriptions. Specimens with purplish panicles, lower glumes 4.5 mm or more and anthers 0.6 mm long or more were designated as *L. aemula* NG (1g–8g) and compared to a selection (10) of *L. aemula* (R.Br.) Trin. specimens from the Great Dividing Range in New South Wales and Victoria (1a–10a). Specimens with green panicles, lower glumes 4.0 mm or less and anthers less than 0.6 mm were designated as *L. filiformis* (1f–21f). Specimens that didn't meet these character sets in all details, were included within *L. filiformis*. Character measurements for one specimen of *Agrostis hirta* Veldkamp (1h) and three specimens of *A. infirma* var. *remota* (Buse) Veldkamp (1i–3i) were also included in the following analysis to serve as related outgroups.

Multivariate analysis was performed on the dataset using the PATN package (Belbin 2013). Because the data consisted of both continuous and discrete variables, it was transformed by the function (Value – Minimum Value)/Range of Value. The analysis used the Gower Metric association measure and classification was by agglomerative hierarchical clustering using the Flexible Unweighted Pair Group Method with Arithmetic mean

Table 1. Morphological characters measured or scored on herbarium specimens of *Lachnagrostis* and *Agrostis* (characters in italics not used in multivariate analysis).

Measurements	Code	Measurements	Code
Vegetative Characters		**Spikelet Characters**	
Leaf roll [1]	Lr	Lower glume total length, mm	Glt
Maximum leaf width, mm [a]	*Lw*	*Upper glume total length, mm*	*Gut*
Flattened leaf width, mm [2]	Lwf	Lower glume:Upper glume length	Gtr
Mid-culm leaf length, cm	Llh	Lemma total length, mm	Lt
Maximum ligule length, mm [a]	Lig	Lemma apex setae, mm	Ls
Inflorescence Characters		Lemma back hairiness [7]	B
Inflorescence habit [3]	Ia	Lemma laterals hairiness [7]	S
Inflorescence height, cm [4]	Ih	Lemma awn attachment, % [8]	Aap
Inflorescence colour [5]	Ic	Awn total length	At
Minimum pedicel length, mm [a]	Pds	Awn column as % of total length	Acp
Maximum pedicel length, mm [a]	*Pdl*	Palea total length, mm	Pt
Median pedicel length [6]	Pdm	Rachilla extension length, mm	Re
		Anther length, mm	A

[1] flat = 1, flat & conduplicate (due to drying) = 2, involute = 3
[2] maximum leaf width*leaf roll
[3] very stiff and erect = 1, rather stiff and more or less erect = 2, not stiff but erect to slightly drooping = 3, lax and weeping = 4
[4] measured from point of emergence from sheath or from lowest whorl if fully emerged
[5] rachis & pedicel colour + spikelet colour/2: light green = 1, mid-green = 2, greyish green (green with minute purple mottling) = 3, mid-purple = 4, dark to reddish purple = 5
[6] (min + max pedicel length)/2
[7] glabrous = 0, occasional hairs only = 1, scattered hairs = 2, covered in hairs but surface still discernible = 3, covered in hairs and surface obscured = 4.
[8] attachment point measured from lemma base
[a] measured to the nearest 0.5 mm

(UWGMA) with a beta value of -0.1 (displayed as a row fusion dendrogram). Ordination was made by Semi-Strong Hybrid (SSH) multidimensional scaling (set at 100 random starts and 500 iterations) and displayed as a 3D ordination plot. Analysis evaluation was made by the calculation of Kruskal-Wallis (KW) values for each resultant group, and Principle Component Correlations (PCC) for each variable.

Testing for significant difference for individual characters between dendrogram subgroups was performed using Excel Data Analysis t-test: Two Sample Assuming Unequal Variances.

A close linear relationship between temperate and altitude exists in NG, which defines a 5.2°C decline in mean maximum (c = 32.67), mean minimum (c = 22.08) and mean annual (c = 27.32) temperatures for every altitudinal increase of 1000 m (Bourke 2017) (e.g. Y_{max} = 32.67 – (0.0052 * a) where Y_{max} = maximum temperature and a = altitude in meters). This relationship was used in an assessment of the climatic ranges for *Lachnagrostis* and *Agrostis*.

Results and Discussion

Between L, BRI and CANB, 54 collections of *Lachnagrostis* were found from PNG and WNG, plus 45 duplicates. Three extra collections (one each) were found at DNA, NSW and MEL and an additional duplicate was found at MEL. All of these specimens had been previously included in *Agrostis avenacea* Gmel. (syn. *Lachnagrostis filiformis* (G.Forst.) Trin.) (Van Royen 1979; Veldkamp 1982; Johns et al. 2006): a grass with widespread natural distribution through Australasia and Malesia but an invasive species in the Americas, parts of Asia, Europe and elsewhere. Apart from *L. filiformis*, collections of *A. infirma* Buse var. *infirma* (syn. *A. rigidula* Steud. var. *rigidula*, *A. sozanensis* var. *exaristata* Hand.–Mazz.), *A. infirma* var. *remota* (Buse) Veldkamp (syn. *A. stricta* (Roem. & Schult.) Buse non J.F.Gmel. var. *remota* Buse, *A. reinwardtii* H.C.Hall ex. Miq., *A. rigidula* var. *remota* (Buse) Hoynck & J.M.Linden), *A. hirta* Veldkamp, *A. clavata* Trin. and *A. gigantea* Roth have been made from NG. The last three taxa were represented by one

Table 2. Means and ranges for measured and scored characters for *Lachnagrostis* and *Agrostis* specimens.

Character	*L. aemula* NG	*L. aemula* Aust	*L. filiformis* NG	*A. hirta* NG	*A. infirma*[1] NG
Lr	1.1 (1–2)	1	1.1 (1–2)	3	1.7 (1–2)
Lw, mm	3.1 (1.5–4)	4.3 (3–6.5)	3.2 (1–5.5)	1.5	2.0 (1–3.5)
Lwf, mm	3.3 (2–4)	4.3 (3–6.5)	3.3 (1.5–5.5)	4.5	2.8 (2.0–3.5)
Llh, cm	18 (10–28)	15 (8–22)	15 (7–26)	13	10 (6–12)
Lig, mm	5.8 (3–10)	6.0 (3.5–11)	5.6 (2–9)	9	3.7 (3–4)
Ia	2.1 (1–3)	2.0 (1–3)	3.3 (2–4)	4	2
Ih, cm	22 (15–29)	27 (19–24)	28 (113–42)	30	18 (15–22)
Ic	6.0 (5–7.5)	5.5 (4.5–6)	4.2 (1.5–6)	8	5.0 (3–7.5)
Pds, mm	1.8 (1–3)	3.3 (1.5–5)	1.1 (0.5–3)	1.5	1.5 (1–2)
Pdl, mm	8.6 (7–13)	13.5 (7.5–13)	5.7 (3–10)	5.5	5.2 (5–5.5)
Pdm, mm	5.2 (4.0–7.3)	8.4 (4.5–11.5)	3.4 (2–5.5)	3.5	3.3 (3.3–3.5)
Glt, mm	4.7 (4.4–5.1)	4.8 (4.0–5.5)	3.5 (3.0–4.5)	3.7	3.6 (2.7–4.3)
Gut, mm	4.1 (3.8–4.6)	4.2 (3.3–5.0)	3.1 (2.6–3.8)	3.7	3.3 (2.5–4.0)
Gtr	1.1 (1.1–1.2)	1.1 (1.1–1.2)	1.1 (1.1–1.2)	1.0	1.1
Lt, mm	2.2 (2.0–2.5)	2.2 (1.7–2.6)	1.7 (1.5–2.0)	2.4	2.4 (2.0–2.7)
Ls, mm	0.2 (0.1–0.5)	0.2 (0.0–0.5)	0.1 (0.0–0.2)	0.1	0.0
B	3.3 (1–4)	4	2.3 (0–4)	0	0
S	3.8 (3–4)	4	3.0 (1–4)	1	0
Aap, %	56 (48–64)	50 (38–62)	52 (41–67)	42	52 (40–60)
At, mm	5.3 (4.4–6.5)	7.0 (5.8–8.1)	4.3 (3.0–5.7)	4.7	3.4 (2.0–4.2)
Acp, %	30 (27–34)	32 (27–34)	31 (24–43)	32	37 (35–39)
Pt, mm	1.9 (1.7–2.2)	1.8 (1.4–2.3)	1.4 (1.2–1.8)	1.3	0.0
Re, mm	1.6 (1.2–1.9)	1.9 (1.5–2.3)	1.0 (0.6–1.5)	0.0	0.0
A, mm	0.7 (0.6–0.8)	0.7 (0.4–0.9)	0.4 (0.3–0.6)	1.0	0.9 (0.7–1.0)

[1] var. *remota*

collection each: *A. hirta* assumed to be an endemic and the other two as introductions. Relatively few collections were identified as *A. infirma* var. *infirma* (spikelets usually 1.9–2.8 mm, awnless: Veldkamp 1982 as *A. rigidula* var. *rigidula*), as the majority were determined as var. *remota* (spikelets usually 3–4.5 mm, awns 2–5.5 mm: Veldkamp 1982 as *A. rigidula* var. *remota*). This more common variety of *A. infirma* in NG is also found in Sumatra and Java, while the typical variety is common to Taiwan, Timor, Java, Celebes, and the Philippines (Veldkamp 1982). The numbers of *A. infirma* var. *remota* collections from NG were approximately twice as many as those of *L. filiformis*.

Morphology

Most character states were variable between specimens of the same taxon, displaying a range of measurements or scores (Table 2). Mean Coefficients of Variation (CV) across all characters (original measures, not derived) were 20% for *L. aemula* from NG, 19% for *L. aemula* from Australia and 27% for *L. filiformis*. The highest variations were for leaf length (Llh), ligule length (Lig), lemma back hairiness (B), lemma setae length (Ls) and minimum pedicel length (Pds). Some of this variation, and particularly that associated with vegetative characters, may be attributable to plasticity in phenotype response to climatic variation (Brown 2012), but whether such plasticity is sufficient to bridge the gap between currently circumscribed taxa within *Lachnagrostis* is untested to date. Definitive differentiation between the two species is not always clear (VicFlora 2018), though they can be easily separated at the extremes of their character ranges.

Multivariate analysis (ordination stress value 0.1259) resulted in a clear separation of NG *Agrostis* from *Lachnagrostis* and of *L. aemula* from *L. filiformis* in both the dendrogram (Figure 1) and for coordinates 1 and 2 of the ordination plot (Figure 2). A clear separation of *A. hirta* from *A. infirma* was also found for coordinate 3 (not shown). All of the Australian *L. aemula* were grouped with the collections from NG, with most separated into a subgroup (Figure 1). The two methods of analysis (i.e. hierarchical clustering and ordination) ranked characters differently in separating taxa (Table 3). For hierarchical clustering, the first eight ranked characters (i.e. those with the highest KW values) were rachilla extension length, anther length, median pedicel length, lower glume (i.e. spikelet), lemma (i.e. floret) and palea lengths, lemma awn length and minimum pedicel length. The first eight ranked characters for ordination analysis (i.e. those with r^2 values > 75%) were rachilla extension, lemma, lower glume and awn lengths, hairiness of the lemma back and laterals, inflorescence habit and median pedicel length. The high ranking of rachilla extension length (Re) in multivariate analysis was unexpected, as it is rarely used as a diagnostic character.

Panicle colouration was not a major character in the differentiation of the hierarchical clusters or in the ordination analysis (Table 3). Although *L. aemula* can have distinctly purple and stiffly divergent inflorescences (Jacobs & Brown 2009), these characters are not always discernible on pressed specimens where colours can be faded and the stage of emergence and age, as well as the style of mounting, can mask the true inflorescence habit. Purpling of the inflorescence was generally stronger in the NG *L. aemula*, compared to *L. filiformis*, but about a third of the latter also displayed strong colouration (Table 2). The greater purpling of both *L. aemula* and *L. filiformis* in the NG specimens may be a response to lower temperatures and higher light intensities or duration (Chalker-Scott 1999), particularly at the higher altitudinal end of their habitats.

Character measurements of NG *L. filiformis* were largely consistent for the taxon as described for Australia (Jacobs & Brown 2009). However, two specimens (19f,

Table 3. Kruskal-Wallis (KW) scores and r-squared values for Principle Coordinate Correlations (PCC) from PATN multivariate analysis of *Lachnagrostis* and *Agrostis* morphological character assessment.

UWGMA KW scores				PCC r-squared values			
Re	34.31	Ia	21.52	Re	0.850	Gtr	0.457
A	32.18	Ic	18.59	B	0.848	Ih	0.417
Pdm	29.37	Lr	16.07	S	0.833	Ls	0.376
Glt	29.07	Lig	12.39	Lt	0.828	Lr	0.343
Lt	27.39	Llh	8.31	Glt	0.822	Lwf	0.274
Pt	26.48	Aap	7.89	Ia	0.816	Ic	0.273
At	26.15	Acp	7.75	At	0.803	Llh	0.253
Pds	25.95	Ih	7.64	Pdm	0.758	Acp	0.179
S	24.12	Gtr	7.19	Pds	0.683	Aap	0.109
B	23.32	Lwf	6.65	Pt	0.600	Lig	0.093
Ls	22.39			A	0.544		

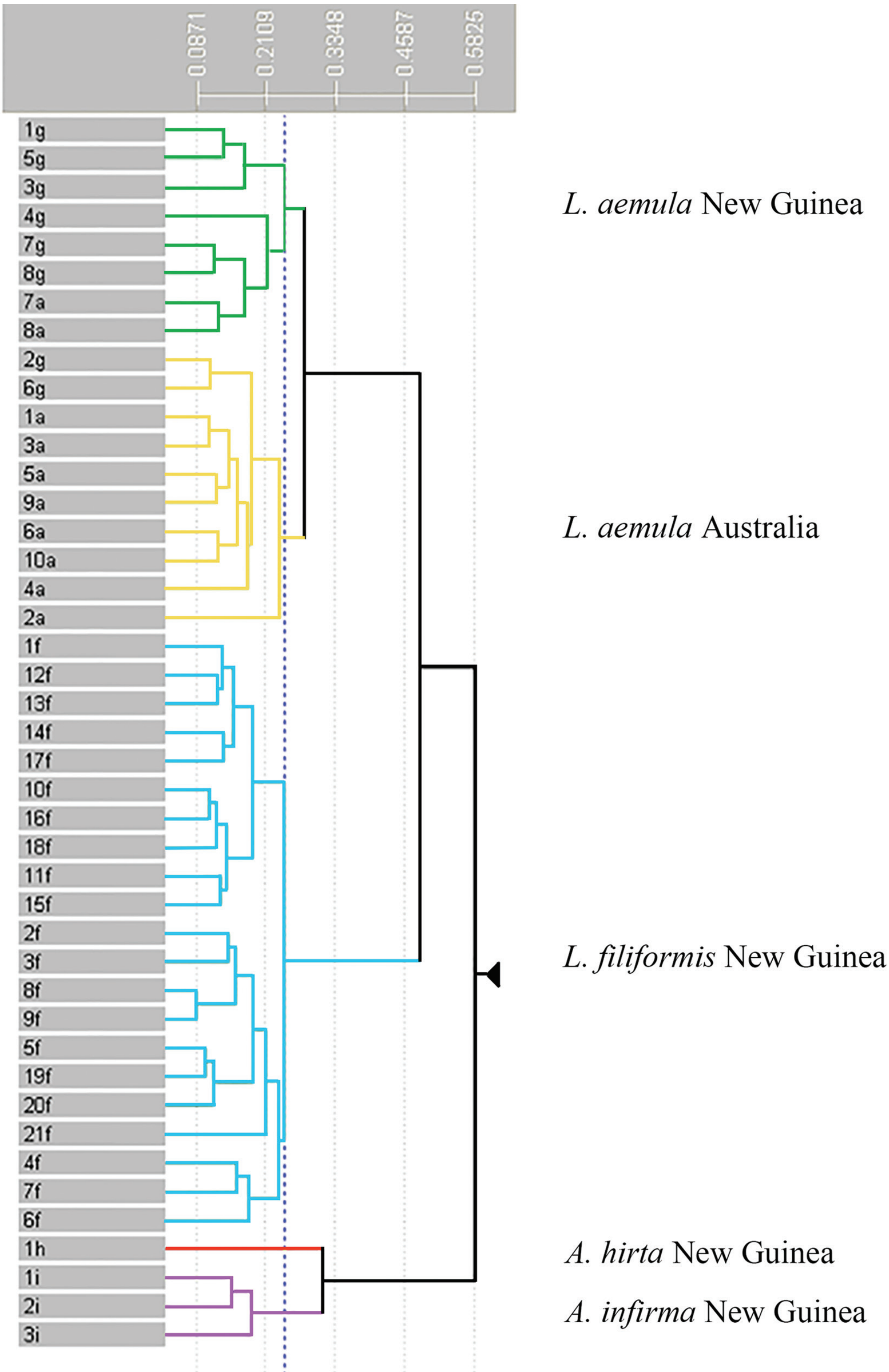

Figure 1. PATN Row Fusion Dendrogram from Unweighted Pair Group Method with Arithmetic Mean (UWGMA) Hierarchical Clustering analysis of *Lachnagrostis* and *Agrostis* morphological character assessment.

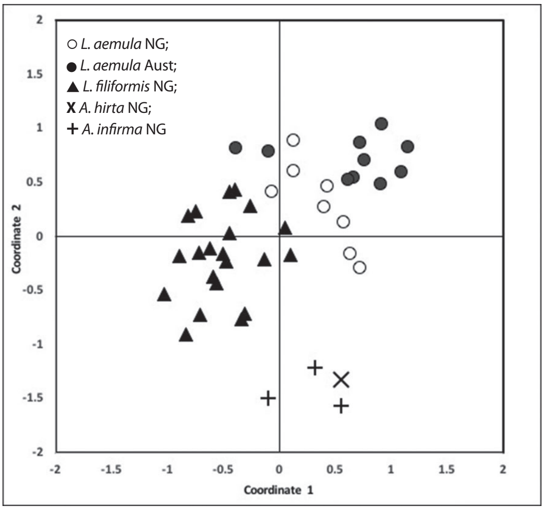

Figure 2. Coordinates 1 and 2 graph of *Lachnagrostis* and *Agrostis* morphological character assessment using PATN Semi-strong Hybrid (SSH) multidimensional scaling ordination: NG = New Guinea, Aust = Australia.

20f) were found to have larger anthers (0.6 mm) than typical and one of these (19f) also had larger than normal spikelets (4.5 mm). Ordination plotting placed these specimens closer to *L. aemula* than the other *L. filiformis*, but the dendrogram had them well embedded within *L. filiformis* (Figure 1). Although the dendrogram split *L. filiformis* into two subgroups, and t-testing (detailed results not given) showed significantly longer spikelets, rachilla extensions, lemma awns and hairier lemmas for the second subgroup compared to the first, the ranges in values showed large overlaps (e.g. spikelet lengths of 3.0–3.7 mm for subgroup 1 and 3.0–4.5 mm for subgroup 2).

The NG specimens of *L. aemula* had significantly shorter rachilla extensions, lemma awns and pedicels (both shortest and median) compared to the Australian specimens. Two Australian specimens of *L. aemula* (7a and 8a) were grouped with the NG specimens in the dendrogram (Figure 1), based on their relatively small spikelets (4.0–4.2 mm). These two collections were made from East Gippsland and may represent a local variant. Two NG *L. aemula* (2g and 6g) were grouped with the Australian specimens (Figure 1), seemingly based on their relatively longer pedicels (6.3–7.3 mm median). Whereas all the Australian and PNG *L. aemula* specimens had densely hairy (score 4) lemmas, two of the four WNG *L. aemula* had lemma backs with near glabrous (score 1) to scattered hairs (score 2) (Table 2). These specimens also had a slightly higher mean spikelet length (4.9 mm compared to 4.5 mm) and stronger purpling than the rest of the NG specimens. As for *L. filiformis*, despite some t-test statistically significant morphological differences among *L. aemula* collections, the ranges in the characters usually overlapped (e.g. total awn length ranged from 4.4–6.5 mm for specimens from NG compared to 5.8–8.1 mm from Australia) (Table 2). Without field observation, a broader base of collections, common nursery trials or supportive DNA evidence, it seems best not to separate any of these *L. aemula* collections into subspecific taxa, at this time.

Habitat

In NG, the *Lachnagrostis* and indigenous *Agrostis* collections have been made between 1700 and 3700 m alt. (mean of 2397 m) (calc.: high altitudinal at 23.8°C mean max to 13.2°C mean min to uninhabited zones at 13.5°C mean max, 2.9°C mean min). While *L. filiformis* and *A. infirma* var. *remota* have been collected across this range (with the single collection of *A. hirta* being from 2286 m alt.), *L. aemula* collections have only been made from 2800 m alt. and above (mean of 3366 m) (calc.: from 18.1°C mean max and 7.5°C mean min and

Key to *Lachnagrostis* and *Agrostis* species of New Guinea used in this paper.

1	Palea absent or less than ½ as long as the lemma; rachilla extension absent or minute and glabrous	2
1:	Palea at least ¾ as long as the lemma; rachilla extension well developed and hairy	3
2	Palea more than 1 mm long; spikelets strongly purple	***Agrostis hirta***
2:	Palea absent or minute; spikelets green to purplish	***Agrostis infirma****
3	Anthers (0.6–) 0.7–0.8 mm long; spikelets (4.2–)4.5–5.2 mm long; rachilla extension (including hairs) 1.4 mm or longer; longest pedicels at least 7 mm long	***Lachnagrostis aemula***
3:	Anthers 0.3–0.4 (–0.6) mm long; spikelets 3.0–4.0(–4.5) mm long; rachilla extension (including hairs) less than 1.4 mm long; longest pedicels usually less than 8 mm long	***Lachnagrostis filiformis***

* includes both New Guinea varieties

colder). None of these species have been collected from the year-round hot, humid Lowlands (calc.: lowlands to intermediate altitudinal zones at 29.6°C mean max, 15.8°C mean min).

Although, *L. filiformis* in Australia is typically a species of temperate grasslands, swamps, stream and lake edges and woodlands, it will grow in arid environments around bores and along creeklines in wet seasons. Despite a flowering season over summer, the species appears to withstand hot daytime temperatures, provided its roots are kept cool (e.g. edge of creeks and waterholes) and winters are mild during its growing season. It also grows in subtropical Queensland, and occasionally in tropical north Queensland (AVH 2018), but at higher altitudes and particularly where permanent water is available (e.g. spring-fed soaks).

The typical form of *L. aemula* is largely confined to wet temperate forests and some dry sclerophyll forests of the Great Dividing Range of Eastern Australia and Tasmania. The wet forests receive more than 889 mm annual rainfall with at least 51 mm per month (Paton & Hosking 1975). Those of Victoria and Tasmania and at higher altitudes (above 700 m) in New South Wales typically have mild to warm summers (18–21°C Jan max, 8–13°C Jan min) and mild to cold winters (9–13°C July max, 2–5°C July min). These temperatures are only slightly higher than those found at the lower end of the altitude range for *L. aemula* in NG. At lower altitudes in New South Wales, summers are hot to very hot (26–27°C Jan max, 12–16 °C Jan min) and not supportive of *L. aemula*. Dry forests typically have 605–867 mm annual rainfall, January temperatures from 22–33°C Jan max and 11–19°C min and July temperatures of 9–16°C max and -0.5–4.5°C min (Newman 1970) and therefore, it is only in the wetter and cooler examples of these, that typical *L. aemula* will grow. Other more robust forms of *L. aemula* can withstand higher temperature regimes in western Victoria and South Australia (Brown in preparation).

Because the majority of *L. filiformis* collections in NG have come from anthropological sites (e.g. roadsides, clearings, gardens), it has been suspected to be an introduced species (Veldkamp 1982). However, as the species only occurs in the Highlands, where it was found growing in the early years of European exploration, it could hardly have been introduced by the same. Although the people of the Highlands are somewhat isolated from those of the Lowlands and often from those in adjacent valleys, goods were traded throughout NG, long before European encroachment (Brown 1978). Apart from a few isolated collections from near Cairns in North Queensland, the nearest common source of *L. filiformis* to NG is south-east Queensland. The species does not appear to be indigenous to western Malesia, with only two small collections from Mt Tatamailau, East Timor in 1954 and two collections from Mt Kinabalu, Borneo in 2001 (BioPortal 2018). The species is native to New Zealand and has been collected from a few Australasian Pacific islands (e.g. Mount Koghi, New Caledonia, 1061 m alt.; Mount Gower, Lord Howe Island, 875 m alt.; Norfolk Island; Kermadec Islands; Chatham Islands), and even as far as Easter Island in the south-east Pacific (AVH 2018), so it possible that the prehistory origins of *L. filiformis* in NG came by way of accidental seed introduction via seafaring traders. However, given the barrier of the humid Lowlands, this does seem improbable. It is more likely that if the species was introduced to the Highlands, it would be by migratory wetland birds.

NG Highlanders practice shifting cultivation, which means that land is cleared for a garden for only one or two harvests before leaving it to bush regrowth for the next 20 to 50 years (Paijmans 1976, Brown 1978). As a result, and although *L. filiformis* is primarily a pioneer species of bared ground, it likely has only a short-term existence on sporadic pockets of cleared land and on the edges of existing gardens, before these sites are taken over again by regrowth. However, with enough interconnected gardens throughout the Highlands and perhaps more permanent sites to supply seed. (e.g. edges of streams and lake beds, roadside verges and ditches), it has managed to persist for at least 100 years, if not thousands of years. The species does not commonly grow at very high altitudes, with only four collections (less than 10%) from above 3000 m alt. In Australia, *L. filiformis* does not grow above the snowline, which at about 1000 m alt., is well below the same in NG.

The *L. aemula* sites in NG are at altitudes higher than that suitable for agriculture. Therefore, this species is even more likely than *L. filiformis* to be indigenous. It is mainly found in wet ground (e.g. stream edges, boggy ground) in grasslands and forest glades. Two collections were made from "dry ashy soils of a native rock shelter" on Puncak Trikora but this may just reflect conditions at the time of observation. These rock shelters are largely used by hunters and collectors, rather than being permanently occupied (Brown 1978). With relatively few collections made, *L. aemula* is likely to be an uncommon species in NG and whether it represents an example of relictualism, is unknown. Like all *Lachnagrostis* species, *L. aemula* is not a competitive grass and in Australia, it does not survive well in improved and grazed pastures. However, unlike *L. filiformis*, it is not usually a coloniser of bared agricultural ground and has not achieved the 'weedy' status of the former (Warnock et al. 2008). The species is largely confined to relatively undisturbed sites, although it can be occasionally found on the verges of mountain roadsides and probably responds favourably to bushfire events (Kitchin et al. 2013).

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Appendix 1: Collections of ***Lachnagrostis*** and ***Agrostis*** assessed for morphological characters.

Taxon	Collections assessed [1]
Lachnagrostis aemula	***New Guinea***: **1g** – Sugarloaf complex along the Wapu River, PNG, 2896 m, 13.vii.1960, *Hoogland & Schodde 7052* (L0837046); **2g** – Wilhelmina-top, WNG, 3560 m, ix.1938, *Brass & Meyer-Drees 9821* (L0837063); **3g** – Wilhelmina-top, WNG, 3700 m, ix.1938, *Brass & Meyer-Drees 10116* (L0837061); **4g** – Wilhelmina-top, WNG, 3650 m, ix.1938, *Brass & Meyer-Drees 9969* (L0837062); **5g** – Mt Trikora, WNG, 3450 m, 17.viii.1984, *Mangen 1107* (L0837059); **6g** – Mt Albert Edward, PNG, 3680 m, v.1938, *Brass 4400* (AQ226576); **7g** – McNicoll–Andabare Plateau, PNG, [2600 m], 22.viii.1960, *Robbins 3336* (CANB87706a); **8g** – Mt Sugarloaf grasslands, PNG, 2896 m, 29.vi.1960, *Robbins 2761* (CANB87781). ***Australia:*** **1a** – Namadgi Nat. Park, NSW, 1175 m, 13.xii.2013, *Walsh 8119* (MEL2378431); **2a** – Nundle to Crawney Pass, NSW, 720 m, 6.xii.1996, *Hosking 1377* (MEL303346); **3a** – Queanbeyan to Williamsdale railway easement, ACT, 745 m, 13.xi.1996, *Crawford 4006* (MEL2212073); **4a** – Sheba Dam, NSW, 1153 m, 5.xii.2009, *Hosking 3287 & Brown* (MEL2366247); **5a** – Mt Gingera, ACT, 1855 m, 17.i.1958, *Burbridge 5611* (MEL1576691); **6a** – Dandenong Ranges, Vic, 305 m, 30.xi.1957, *Muir 274* (MEL1055530); **7a** – Metung Rd, Lakes Entrance, Vic, [62 m], 27.xi.1960, *Muir 1975* (MEL1055531); **8a** – Newry Hill Climb, Vic, [78 m], 21.x.1984, *Beauglehole ACB78705* (MEL1533249); **9a** – Langwarrin Railway Station, Vic, [78 m], 28.xi.1978, *Corrick 6206* (MEL1509861); **10a** – Mt Buffalo [2], Vic [671 m], 19.xi.1987, *Beauglehole ACB92328* (MEL1590071).
Lachnagrostis filiformis	***New Guinea:*** **1f** – Sirunki, Putidi Hill, PNG, 2591 m, viii.1962, *Walker ANU456* (L0837609); **2f** – Gembogi, Chimbu Valley, PNG, 2134 m, 13.ix.1971, *Wace ANU13020* (L0837065); **3f** – Mt Kaindi summit, PNG, 2250 m, 16.i.1993, *Hoft 3281* (L0393732); **4f** – Edie Creek, PNG, 1981 m, 7.xi.1966, *Ridsdale s.n.* (L0837044); **5f** – NE of Lake Habbema, WPG, 2800 m, x.1938, *Brass 10726* (L0837065); **6f** – Lake Myola, PNG, 1921 m, 5.xi.1964, *Gillison 409* (L0837060); **7f** – Yobobos grassland area, PNG, 2591 m, 24.viii.1960, *Hoogland & Schodde 7579* (L0837057); **8f** – Lake Myola, PNG, 2000 m, 22.vii.1974, *Croft et al. LAE61936* (L0837052); **9f** – Mt Kenive, PNG, 2400 m, 2.viii.1974, *Croft et al. LAE65225* (L0837051); **10f** – Alipe, Kepaka, Upper Kaugel Valley, PNG, 2134 m, 25.i.1973, *Bowers 847* (L0837067); **11f** – Urunu, Vanapa Valley, PNG, 1900 m, vii.1933, *Brass 4783* (L0837066); **12f** – Mt Wilhelm, PNG, 2600 m, x.1938, *Brass 30777* (L087064); **13f** – Kombugomambuno, Mt Wilhelm, PNG, 3330 m, 2.viii.1984, *Kerenga & Garki 56864* (L0837058); **14f** – Pass between Mt Nee and Mt Kerewa, PNG, 2890 m, 13.vii.1966, *Kalkman 4875* (L087056); **15f** – Quinane Nursery, Aiyura, PNG, 1829 m, ii.1953, *Womersley 5121*, (AQ226400); **16f** – Daulo Road Camp, Chimbu Pass, PNG, 2438 m, *Womersley et al. 6090* (AQ226399); **17f** – Kergsugl to Mt Wilhelm, PNG, 2591 m, 2.vii.1970, *Willis s.n.* (MEL572651); **18f** – Tomba, PNG, 2438 m, 29.vi.1957, *Saunders 639* (MEL571234); **19f** – Kumbapuku, Kepake, PNG, 2225 m, 8.xi.1968, *Bowers 309* (CANB199808); **20f** – Kambia Village, Kandep Valley, PNG, 2256 m, 12.viii.1960, *Robbins 3271* (CANB87740); **21g** – Mt Gilwe, PNG, 3658 m, 17.vii.1967, *Coode NGF32545* (L0837043).
Agrostis hirta	**1h** – Sugarloaf complex along the Wapu River, PNG, 2286 m, 13.vii.1960, *Hoogland & Shodde 7046* (CANB83908).
Agrostis infirma var. *remota*	**1i** – McNicoll–Andabare Plateau, PNG, [2600 m], 22.viii.1960, *Robbins 3336* (CANB87706a); **2i** – Pinaunde River, PNG, 3505 m, 17.vi.1968, *Vandenberg NGF39564* (AQ226404); **3i** – Mt Gilwe, PNG, 3200 m, 25.xii.1973, *Croft et al. LAE60689* (AQ353578).

[1] Altitude in feet converted to metres with missing data in brackets estimated from location description and Google Earth.

[2] No definite location or habitat details provided – alt. of collection is therefore taken to be half way up the mountain.