Association of five *Austrodanthonia* species (family Poaceae) with large and small scale environmental features in central western New South Wales.

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Abstract: Twenty-eight natural populations of Wallaby Grasses, *Austrodanthonia* species, in central western New South Wales were sampled and species presence related to a suite of environmental characteristics. An average of 12 plants were selectively sampled from each population; most populations consisted of at least four out of five species, *Austrodanthonia bipartita*, *A. caespitosa*, *A. eriantha*, *A. fulva* and *A. setacea*. Numerous ecological factors allowed the widespread co-occurrence of these closely-related species. Large-scale rainfall and climatic factors were correlated with species-presence but no universal small-scale site environmental variables were important for all species. The most widespread species was *Austrodanthonia caespitosa* and environmental variations at a local site scale, depending on exposure to solar radiation, may at least partially overcome regional rainfall and climate influences.

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Introduction

Wallaby Grasses (*Austrodanthonia*) are widespread native perennial grasses of economic importance to large areas of Australian temperate native grasslands but are of particular importance in south-eastern Australia (Vickery 1956; Groves & Whalley 2002). As a group, Wallaby Grasses are recognised as being persistent and productive (Lodge & Schipp 1993; Groves & Whalley 2002; Garden *et al*. 2005; Waters *et al*. 2005), as well as being one of the more palatable and nutritious of the native grasses (Cashmore 1932; Williams 1961; Scott & Whalley 1982; Archer & Robinson 1988; Robinson & Archer 1988; Lodge & Whalley 1989; Lodge 1993; Groves & Whalley 2002). Species within this genus also appear to have 'resilience' to changes in soil fertility and grazing brought about by agricultural practises (Oram & Lodge 2003), and have been reported to have a capacity to successfully colonise disturbed croplands and pastures (Garden *et al*. 2001) even under summer drought conditions (Dear *et al*. 2006; Hackney *et al*. 2006; Waters *et al*. 2007). The most widespread species in the genus, *Austrodanthonia caespitosa*, grows across a broad range of environments. The scale of ecotypic variation for this species is unclear with some studies finding evidence for large scale variation (Hodgkinson & Quinn 1976; Quinn & Hodgkinson 1983) and others showing variation over much smaller scales of variation (Waters *et al*. 2003). Apart from difficulties resulting from the scales at which environmental factors are measured, some of the confusion over the environmental requirements of species may also be a result of grouping different species together due to difficulties in species identification. For example, *Austrodanthonia caespitosa* has a taxonomic affinity with a number of different species in the genus (Vickery 1956) and is often described as a 'very variable' species (e.g. Wheeler *et al*. 2002). This makes grouping species within *Austrodanthonia* an appealing option, particularly for vegetation surveys.

Since accounts of environmental factors influencing the occurrence of this species have not been reported, it has not been possible to assess the true breadth of environments *Austrodanthonia caespitosa* or other closely-related species in the genus occupy. Inadequate information on environmental factors affecting species distribution has led to some confusion over the scales of adaptation within *Austrodanthonia*. For example, in a farm survey in the NSW Southern Tablelands, Garden *et al*. (2001) did not find a significant association of *Austrodanthonia* with soil pH although, generally, the genus was associated with higher pH soils. Similarly, in a survey of natural and improved pastures in the Goulburn district, Munnich *et al*. (1991) also found no relationship between abundance of *Austrodanthonia* and soil pH. However, they suggest that, due to its local abundance and the prevalence of acid soils in the area, at least some species in the genus may exhibit acid tolerance. Both Rubzen *et al*. (1996) and Dowling *et al*. (1996) report large differences in acid tolerance between *Austrodanthonia* species; these differences have been highlighted in subsequent studies by Islam (2002). Soil type was shown to

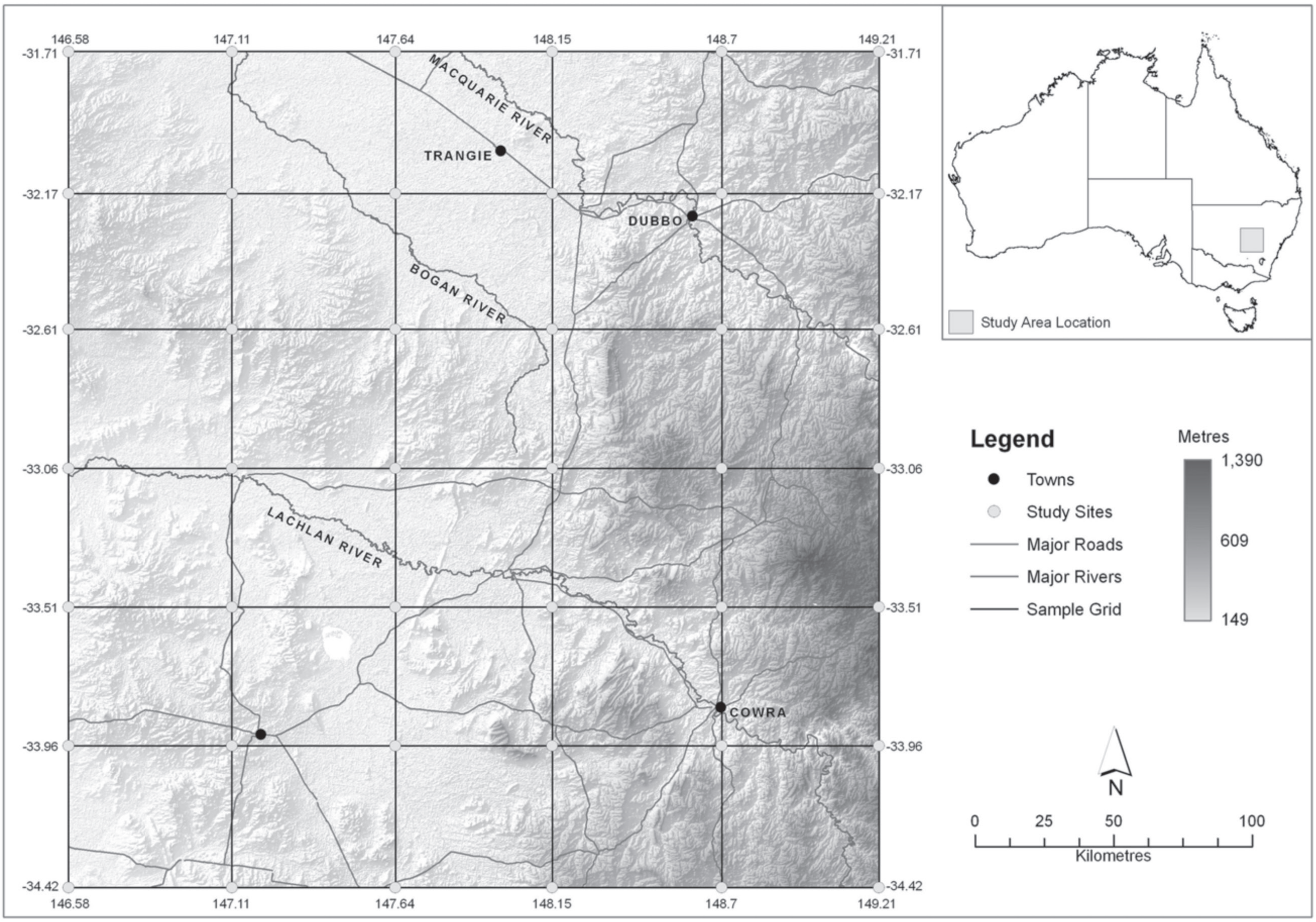

Fig. 1. Study area for *Austrodanthonia* collection. The area has a rainfall gradient from higher AAR, (600 – 800 mm) in the east, to lower (400 mm) in the west. Seasonality of rainfall also changes across the area with southern localities representing more cool-season dominant rainfall and northern localities typically aseasonal rainfall. Cross-points represent a locality (population).

have a negligible influence on *Austrodanthonia* occurrence in Garden *et al*. (2001), but shown to be significant in other studies (Scott & Whalley 1982; Robinson *et al*. 1993). Scott and Whalley (1982) surveyed six species from nine sites on the New England Tablelands and found each species occupied a distinct ecological niche associated primarily with geology (parent material), but also soil texture and total soil phosphorus.

Hodgkinson and Quinn (1976) examined populations along a north-south transect from northern NSW to Tasmania, and found declining relative growth rates with increasing latitude. Garden *et al*. (2001) found the distribution of different *Austrodanthonia* species to be influenced by latitude but suggested these differences were more a reflection of variation in agricultural practices and grazing intensity than rainfall. The potential importance of grazing intensity was also highlighted in the New England Tablelands (Scott & Whalley 1984). Here, populations of three *Austrodanthonia* species, *A. bipartita, A. richardsonii* and *A. racemosa* growing within high grazing intensity/high fertility sheep camp sites had a greater number of shorter tillers and later flowering times than adjacent populations growing away from sheep campsites. They point out that such micro-habitat differentiation may have occurred in a relatively short period of time, perhaps within 30 years. Alternatively Oram and Lodge (2003) suggest that genotypes of *Austrodanthonia* tolerant of high intensity grazing/high fertility are likely to have been present in pre-settlement populations. Studies such as Scott and Whalley (1984) and Hodgkinson and Quinn (1976) show that drawing relationships between species distribution and environmental factors will be influenced by the type and scale at which landscape variables are measured.

The plant material described in this paper documents the collection of parent plant material for a larger genecological study aimed to determine the scale of adaptation in *Austrodanthonia caespitosa* and four closely related species *Austrodanthonia bipartita*, *A. eriantha*, *A. fulva* and *A. setacea*. As geographic patterns of genetic variation often underpin factors important in determining processes of genetic variation and the generation ecotypic variation (Coates & Byrne 2005) an understanding of the environmental requirements of these species is required before any insights to genetic structure of populations can be made. Here we assess the breadth of environments occupied by *Austrodanthonia caespitosa* and other closely related species and describe the plant collection methods for a larger

Table 1. Locality description for each population of *Austrodanthonia* collected from central western New South Wales.

Locality no.	Pop'n name	Lat.(-)	Long.	No. plants coll.	Abip[1]	Acap	Aeri	Aful	Aset	MAR[2] (mm)	Max. Temp (ann.) (0^c)	Et (mm) (ann.)	Rh (%) (ann.)	No. Sun hrs (ann.)	Mean Alt.[3] (m)	Class	Soil surface text.[2]	Class. text're	Collection numbers[4]
1	Hermidale	31.71	146.58	15	✓			✓		437	25.1	431.0	59.8	8.7	252	Imported	coarse	11	1.11;1.15
2	Nyngan	31.71	147.11	19	✓	✓		✓		453	25.5	449.6	61.0	8.6	178	Imported	coarse	11	2.13
3	Nevertire	31.71	147.64	20	✓	✓		✓	✓	481	25.2	464.5	62.9	8.2	194	Imported	coarse	11	3.01;3.14;
4	Collie	31.71	148.15	11	✓			✓	✓	524	24.8	493.7	65.1	8.1	217	Imported	coarse	11	4.01;4.03
5	Gilgandra	31.71	148.70	15	✓	✓	✓	✓	✓	570	24.4	545.1	66.6	8.0	336	Imported	fine	12	
6	Mendooran	31.71	149.21	13		✓		✓	✓	677	23.4	589.6	67.6	7.9	440	Imported	fine	12	6.04
7	Nymagee	32.17	146.58	6	✓			✓	✓	454	24.4	437.1	61.5	8.5	244	Imported	fine	12	7.16
8	Tottenham	32.17	147.11	14	✓	✓		✓		465	24.9	451.6	62.8	8.3	206	Imported	coarse	11	8.02;8.18
9	Trangie	32.17	147.64	17	✓	✓		✓	✓	506	24.7	469.6	64.2	8.0	202	Imported	coarse	11	9.02;9.07
10	Narromine	32.17	148.15	13	✓	✓		✓	✓	545	24.3	505.5	65.4	8.0	235	Sediment	coarse	21	10.08
11	Dubbo	32.17	148.70	6	✓	✓		✓		588	24.0	547.8	67.9	7.9	342	Igneous	fine	32	
12	Dunedoo	32.17	149.21	7	✓	✓		✓	✓	630	23.4	601.1	69.5	7.8	722	Sediment	fine	22	12.01;12.18
13	Bobadah	32.61	146.58	11	✓	✓		✓		435	24.2	439.0	62.6	8.4	278	Imported	coarse	11	13.1;13.15
14	Boona	32.61	147.11	17	✓	✓		✓	✓	541	23.5	466.6	64.1	8.2	288	Metasediment	coarse	41	14.02;14.07
15	Tullamore	32.61	147.64	10	✓	✓	✓	✓	✓	521	24.3	495.6	65.2	8.0	239	Metasediment	fine	42	15.04;15.12
17	Wellington	32.61	148.70	16	✓	✓	✓	✓		633	23.2	556.0	66.5	7.9	377	Intrusive	coarse	51	17.11;17.13
18	Burrendong	32.61	149.21	14		✓				663	23.2	608.7	69.4	7.7	370	Metasediment	fine	42	18.18
19	Euabalong	33.06	146.58	17	✓	✓			✓	420	24.5	428.8	63.8	8.2	169	Imported	fine	12	19.07;19.09
20	Condobolin	33.06	147.11	9	✓	✓		✓	✓	458	24.2	459.5	64.3	8.0	208	Metasediment	fine	42	20.19;20.20
21	Bogan Gate	33.06	147.64	6	✓			✓		578	23.0	486.7	64.6	7.8	290	Imported	fine	12	21.03;21.14
22	Parkes	33.06	148.15	8	✓	✓		✓		617	22.9	550.5	62.9	7.8	344	Metasediment	coarse	41	22.01;22.18
26	Ungarie	33.51	147.11	11		✓	✓		✓	850	23.6	465.2	65.1	7.8	208	Imported	fine	12	26.19
27	Jemalong	33.51	147.64	4		✓			✓	475	23.7	495.8	65.7	7.7	232	Imported	fine	12	
28	Goologong	33.51	148.15	4		✓				489	23.0	576.5	66.2	7.6	262	Igneous	fine	32	
29	Canowindra	33.51	148.70	8	✓	✓				591	22.3	611.6	67.7	7.5	329	Imported	fine	12	
31	Weethalle	33.96	146.58	17		✓	✓		✓	447	23.5	427.8	65.3	7.8	239	Metasediment	coarse	41	31.01;31.06; 31.07;31.12
37	Barellan	34.42	146.58	20	✓	✓	✓		✓	485	22.8	442.5	67.0	7.7	157	Intrusive	coarse	51	37.13;37.16; 37.19
38	Ariah Park	34.42	147.11	13	✓	✓	✓	✓	✓	562	22.1	481.4	68.1	7.6	281	Igneous	fine	32	38.07;38.15

[1] *Austrodanthonia bipartita* = **Abip;** *A. caespitosa* = **Acap**; *A. eriantha* = **Aeri** ; *A. fulva* = **Aful** ; *A. setacea* = **Aset.**; [2] Mean annual rainfall:[3] GPS determined; [4] Plant specimens lodged in the NSW National Herbarium

genecological study. Specific aims are: i) to determine the association of species with different environmental factors at both the large (locality) and small (site) scales; ii) to compare the range of environments occupied by the five species *Austrodanthonia caespitosa*, *A. bipartita*, *A. eriantha, A. fulva*, A. *setacea*; and (iii) to generate hypotheses about the factors affecting the distribution and abundance of these species.

Methods

Collection of natural populations

Twenty eight natural populations of *Austrodanthonia* spp. were systematically sampled across a 75,000 km^2 collection area at approximately 50 km intervals using 7 parallel east-west and 6 north-south transects between May 2003 and January 2004 (Figure 1). Where possible, 20 plants were collected to represent a population within a 10 km radius of each grid-point (locality). Plants were collected in pairs, consisting of an individual and its nearest neighbour (<1 m apart). Individual plants were chosen to cover the range of environments (sites) within the locality. Localities included roadside verges, native forests, grazed/cropped paddocks, stock routes and cemeteries. Whole plants were collected following the methods described by Whalley and Brown (1973), and transplanted into a nursery at Trangie Agricultural Research Centre (31° 50'S, 1470° 57'E). Due to difficulties in field identification of species, plants were identified following transplanting. Representative specimens were lodged at the National Herbarium of New South Wales in Sydney. Details of populations and localities are in Table 1. Seed heads were bagged on each of the 339 plants collected and progeny grown for use in a subsequent genecological study.

Environmental characteristics

The environment of each population was characterised at two scales; large-scale 'locality characteristics' defined each population, and small-scale 'site characteristics' were specific to the environment in which each plant was growing.

Locality characteristics for each populations included climatic and topographic (Table 1) and soil characteristics (Table 2). A soil core was taken for each locality to a maximum depth of 1.2 m where possible. Where there was an obvious change in soil type or topographic position within a locality, an additional soil core(s) was taken. For each core, a 0–10 cm soil sample of the A horizon was used to determine soil pH, electrical conductivity (EC), total phosphorus (P), potassium (K), sulphur (S), total nitrogen (N) and cation exchange capacity (CEC) (following Rayment & Higginson 1992a, 1992b). Total organic carbon (OC) was determined using the Walkley & Black (1934) method. Where a B horizon existed, its depth was recorded and a second soil sample (top 10 cm of the B horizon) was analysed. The same soil chemical properties as for the A horizon were determined for the B horizon except phosphorus and organic carbon (Table 3). For each sample (A and B horizons), soil texture and colour were measured using the methods of Northcote (1979). Geological data were obtained from the Statewide Geological Geodatabase (Xie 2003). In an attempt to pinpoint the most useful geological data in terms of plant genotypes a non-parametric classification was used to allocate one of eight geological classes (class.texture) to each locality by combining dominant lithology (indicating fertility) with estimated clay content (Table 1).

A total of 18 site characteristics was recorded in the field at the time of plant collection following Austin *et al*. (2000) and are summarised in Table 4.

Data analysis

All analyses were performed using the statistical package R (http://cran.r-project.org).

Univariate analyses

Numeric locality and site variables: Regression models were used to assess whether species (*Austrodanthonia bipartita*, *A. caespitosa*, *A. eriantha*, *A. fulva* and *A. setacea*) was related to numeric locality or site environment variable. Site 19, "Euabalong" was omitted from the analysis of soil data as both the S and EC values in the A-horizon and the EC and Na in the B-horizon were extremely high and could not be explained (Table 2). Predicted means (+se) for each variable were calculated and compared for each species. In all analyses, the residuals from the regression models were examined for normality and constant variance.

Factor locality and site variables: Chi-squared tests were performed to examine the association between each environmental factor and species. Significant associations were explored by comparing the expected plant count (under the null assumption of no association) to the actual plant count.

Multivariate analyses

Stepwise generalised linear models (GLM) were used to examine the set of variables (locality and site variables) that best predicted the occurrence of an *Austrodanthonia* species at a location. For ease of data interpretation, variables were grouped and for each group a separate analysis was undertaken. Four groupings were made, specifically rainfall, climate, soils/geology and all remaining site environment variables. For locality variables, the proportion of a species within a site was defined as the dependent variables using a logit transformation together with a binomial error assumption. For site variables, presence/absence of a species was defined as the dependent variable using a logit transformation together with a binomial error assumption. Terms (numeric and factor), were successively added in a stepwise manner with entry of variables in accordance with the p-value ($p<0.05$).

Table 2. Soil chemical characteristics of A-horizons (0-10 cm) for each locality of 28 populations of *Austrodanthonia* collected from central western New South Wales.

Locality no.	Pop'n name	Site of additional soil samples[1.]	pH[2.] ($CaCl_2$)	EC[3.] (dS/m)	P (mg/kg)	K (mg/kg)	S (mg/kg)	OC %	Exchangable Cations meq/100g[4.] Ca	Mg	Na	K	Al	Total CEC	Total N (mg/kg)
1	Hermidale		6.23	0.24	4	356	4.4	0.95	5.44	2.01	0.17	0.88	0.03	8.53	0.07
2	Nyngan		5.46	1.67	18	593	7.0	1.08	6.77	1.56	0.05	1.48	0.11	9.97	0.10
3	Nevertire		8.64	0.90	31	880	3.7	1.25	16.37	1.62	0.04	2.22	0.03	20.28	0.11
4	Collie		6.27	1.25	11	214	7.1	0.98	10.24	5.86	1.81	0.55	0.03	18.49	0.10
5	Gilgandra[1.]	Flora reserve	6.63	0.35	4	75	3.5	0.63	1.79	0.60	0.06	0.16	0.03	2.64	0.03
		"Yalroo"	5.49	0.17	6	181	3.1	1.63	1.11	0.92	0.09	0.40	0.90	3.42	0.07
6	Mendooran[1.]	Bottom slope	6.66	0.36	9	749	3.6	2.19	12.92	5.97	0.08	1.92	0.05	20.94	0.19
		Top slope	7.22	0.23	5	487	3.6	1.14	7.89	1.81	0.06	1.21	0.04	11.01	0.11
7	Nymagee		6.16	0.15	8	334	2.3	0.78	5.89	1.99	0.04	0.85	0.08	8.55	0.07
8	Tottenham		5.89	0.60	12	559	9.3	1.25	6.67	2.13	0.08	1.38	0.05	10.31	0.11
9	Trangie		5.52	0.59	29	474	8.8	1.34	4.30	1.14	0.05	1.19	0.15	6.83	0.10
10	Narromine		6.89	1.14	8	521	5.2	0.97	11.98	6.68	0.58	1.32	0.04	20.60	0.14
11	Dubbo[1.]	Lower slope	6.87	0.40	11	343	4.5	3.89	15.08	5.50	0.10	0.84	0.03	21.53	0.25
		Upper slope	7.03	0.31	10	141	3.2	3.00	16.34	4.99	0.20	0.36	0.05	21.94	0.18
12	Dunedoo[1.]	Roadside	4.97	0.41	5	128	6.0	1.17	1.07	1.18	0.14	0.32	0.70	4.58	0.09
		State forest	5.23	0.18	7	116	5.6	1.92	0.34	0.74	0.08	0.30	1.14	2.60	0.10
13	Bobadah[1.]	State forest	5.44	0.27	8	621	8.7	1.49	5.73	1.7	0.06	1.52	0.08	9.09	0.11
		Roadside	5.52	0.97	5	300	5.9	1.36	4.29	1.06	0.04	0.75	0.22	6.36	0.10
14	Boona		6.16	0.30	7	492	3.5	1.72	5.87	3.58	0.10	1.26	0.05	10.86	0.11
15	Tullamore		5.09	0.34	8	200	5.0	1.42	2.26	1.93	0.03	0.44	0.99	5.63	0.09
16	Peak Hill[1]	Roadside	7.20	1.13	7	336	6.7	1.59	10.22	8.05	2.07	0.84	0.003	21.18	0.13
		Wooded roadside	6.00	0.25	11	402	4.1	1.91	5.78	2.86	0.26	0.98	0.11	9.99	0.12
17	Wellington[1.]	Roadside	6.88	0.68	5	286	4.4	0.49	3.12	4.27	1.31	0.67	0.01	9.38	0.04
		Wooded roadside	7.52	0.17	7	280	2.5	0.71	6.09	2.39	0.11	0.35	0.01	8.95	0.06
18	Burrendong[1.]	Lion Island	6.08	0.13	20	279	2.6	1.28	5.24	2.27	0.04	0.3	0.14	7.99	0.11
		Foreshore	6.31	0.25	13	433	4.0	1.57	7.37	1.46	0.04	0.36	0.01	9.24	0.15
19	Euabalong		8.99	17.27	78	381	198	1.23	9.48	6.96	11.83	0.89	0.001	29.16	0.12
20	Condobolin[1.]	Roadside	6.65	0.15	7	407	4.6	0.63	5.14	2.68	0.09	1.03	0.002	8.94	0.06
		Research Station	6.68	0.53	14	860	5.0	1.63	7.4	4.44	0.21	2.16	0.002	14.21	0.13
21	Bogan Gate[1.]	Gully	5.20	0.21	10	257	4.1	1.81	0.6	0.73	0.09	0.38	1.04	2.84	0.09
		Upper slope	7.19	1.11	21	898	12.1	2.84	11.44	2.81	0.29	2.21	0.002	16.75	0.14
23	Cumnock[1.]	Crest	6.34	0.25	4	146	4.7	0.75	2.36	0.73	0.07	0.26	0.00	3.42	0.07
		Mid slope	5.34	0.15	4	89	3.7	0.61	2.63	0.67	0.03	0.21	0.02	3.56	0.06
24	Mullion Creek		6.51	0.23	5	155	7.8	0.51	2.19	2.27	0.23	0.24	0.06	4.99	0.07
26	Ungarie		6.58	0.27	9	471	4.3	0.89	4.68	2.3	0.30	1.19	0	8.47	0.10
27	Jemalong[1.]	Lower slope	5.42	0.57	10	433	8.8	1.7	3.3	3.14	0.30	1.09	0.41	8.24	0.14
		Mid slope	5.81	0.74	12	289	11.8	3.56	6.93	3.21	0.40	0.66	0.08	11.22	0.22
		Upper slope	5.65	0.19	11	136	5.3	1.32	1.64	0.77	0.08	0.22	0.32	3.03	0.10
28	Goologong		7.98	1.47	5	602	7.2	0.41	6.89	12.59	1.52	1.49	0.01	22.5	0.09
29	Candowndra[1.]	Cemetery	5.95	0.18	8	330	6.1	1.23	4.74	1.83	0.05	0.68	0.01	7.31	0.14
		Molong Creek	7.20	0.37	8	546	4.7	0.66	8.98	4.58	0.17	1.37	0.00	15.10	0.14
31	Weethalle		5.69	0.17	7	311	4.6	0.96	4.23	1.48	0.03	0.78	0.21	6.73	0.08
37	Barellan		7.04	0.33	5	470	3.2	0.67	6.21	2.80	0.27	1.16	0.003	10.44	0.06
38	Ariah Park		4.59	0.37	6	167	6	1.04	0.84	1.06	0.08	0.36	1.5	3.82	0.08

[1.] Sites where a number of different soil types existed. [2.] 1:5 soil/0.01 M $CaCl_2$ extraction [3.] dS/m, 1:5 soil/water extraction [4.] cmol +/kg $BaCl_2/NH_4Cl$ extraction

Table 3. Soil chemical characteristics of B-horizons for each locality of 28 populations of *Austrodanthonia* collected in central western New South Wales.

Locality no.	Population name	Site of additional soil samples	Soil depth[1] (cm)	pH [2] ($CaCl_2$)	EC [3] (dS/m)	Exchangable Cations meq/100g [4] Ca	Mg	Na	K	Al	Total CEC	Total N (mg/g)
2	Nyngan		63	8.08	1.05	11.18	1.22	0.04	0.75	0.00	13.19	0.04
3	Nevertire		35	8.58	1.03	13.02	5.55	0.25	1.41	0.00	20.23	0.06
4	Collie		50	8.57	6.08	16.21	9.12	6.46	0.47	0.00	32.26	0.06
5	Gilgandra	Flora reserve	60	6.17	0.10	0.56	0.95	0.21	0.13	0.11	1.96	0.04
		"Yalroo"	30	5.59	0.29	0.39	2.94	0.55	0.35	1.31	5.54	0.03
6	Mendooran	Bottom slope	25	8.06	1.10	8.68	2.87	0.08	0.70	0.00	12.33	0.06
7	Nymagee		40	7.55	0.15	7.41	2.24	0.08	0.75	0.00	10.48	0.05
			54	6.58	0.41	5.94	4.16	0.72	0.85	0.00	11.67	0.06
8	Tottenham		36	6.12	0.48	4.12	3.56	0.97	0.63	0.07	9.35	0.06
9	Trangie		34	6.55	0.32	5.07	1.31	0.09	0.77	0.00	7.24	0.06
10	Narromine		35	9.25	2.96	10.05	11.06	3.94	0.40	0.00	25.45	0.04
11	Dubbo	Lower slope	35	6.12	0.19	4.72	4.08	0.18	0.54	0.00	9.52	0.05
		Upper slope	33	6.57	0.14	3.86	3.97	0.16	0.53	0.00	8.52	0.03
12	Dunedoo	Roadside	40	5.07	0.80	0.63	5.46	0.80	0.15	1.17	8.21	0.07
		State forest	40	8.30	3.06	3.45	8.54	1.81	0.12	0.02	13.94	0.05
14	Boona		40	6.59	0.70	4.13	4.21	0.61	0.78	0.00	9.73	0.06
16	Peak Hill	Roadside	30	9.84	5.68	12.23	11.91	6.26	0.46	0.00	30.86	0.06
		Wooded roadside	37	6.81	2.34	7.72	6.79	3.54	0.50	0.00	18.55	0.10
17	Wellington	Roadside	30	8.06	2.39	4.01	9.83	4.43	0.75	0.00	19.02	0.08
		Wooded roadside	30	5.79	0.17	6.91	3.57	0.38	0.31	0.45	11.62	0.03
18	Burrendong	Foreshore	39	7.83	0.43	13.76	4.14	0.12	0.22	0.00	18.24	0.08
19	Euabalong		52	9.23	17.27	6.51	6.66	18.55	0.66	0.00	32.32	0.07
20	Condobolin	Roadside	20	6.27	0.15	3.44	2.26	0.31	0.83	0.01	6.85	0.04
		Research Station	34	8.53	1.29	13.50	5.76	0.65	2.67	0.00	22.57	0.06
21	Bogan Gate	Gully	70	7.62	0.40	6.72	2.86	0.15	0.85	0.00	10.58	0.04
23	Cumnock	Crest	50	5.97	0.20	1.43	2.31	0.12	0.22	0.13	4.27	0.04
		Mid slope	56	6.09	0.09	1.63	1.32	0.05	0.18	0.18	1.73	0.04
24	Mullion Creek		30	7.92	1.16	4.64	6.02	1.29	0.12	0.03	12.10	0.05
26	Ungarie		15	6.96	1.06	6.15	5.91	1.91	1.02	0.00	14.27	0.10
27	Jemalong	Lower slope	20	5.81	0.74	2.61	6.18	1.40	0.97	0.14	11.30	0.09
29	Candowndra	Cemetery	38	6.80	0.15	6.22	2.67	0.07	0.75	0.01	9.72	0.07
		Molong Creek	25	7.63	0.65	8.91	5.24	0.33	1.21	0.00	15.69	0.06
31	Weethalle		23	5.37	0.18	1.88	3.02	1.07	0.54	0.28	6.79	0.04
37	Barellan		70	5.86	0.47	8.52	2.01	0.11	1.18	0.01	11.83	0.13
38	Ariah Park		36	5.85	0.57	4.05	1.07	0.07	0.96	0.01	6.16	0.05

[1] Depth to B horizon. [2] 1:5 soil/0.01 M $CaCl_2$ extraction [3] dS/m, 1:5 soil/water extraction [4] cmol +/kg $BaCl_2/NH_4Cl$ extraction

The simplest significant models are reported with regression coefficients for all numeric variables.

Principal Components analyses (PCA) were used to examine the patterns between species occurrence and numeric environment variables using the same grouping of environmental variables as for the GLM. Soils data from the B horizon were omitted from these analyses because of missing values; this occurred where the B horizon was not evident within the first 1.2 m. The most important variables contributing to the first, second and third principal components (PC1, PC2 and PC3 respectively) and the cumulative proportion of the variation accounted for by each of the three components were determined. The major components from these analyses were then related to species occurrence to determine of any relationships could be found.

Results

Up to five species were recorded at any one location; 72% of populations had three species or more. Specifically, 20% of populations had three species, 31% had four species and 20% had five species. When collecting plants in pairs at 1 m spacing, it was uncommon to find different species. Only two populations contained one species; the "Mullion Creek" population (locality 24) where 20 *Austrodanthonia setacea* plants were collected but only two individuals survived; and the "Canowindra" population (locality 29) that contained *Austrodanthonia caespitosa* only.

Relationships between species and environment

Austrodanthonia caespitosa was associated with localities of higher mean annual rainfall and *A. setacea* with lower

Table 4. Description of site variables measured at the time of collection of *Austrodanthonia* plant pairs.

Site variable	Variable category
GPS position (Northing and Easting)	Continuous variable
Altitude (m)	Continuous variable
Slope (°)	Continuous variable
Aspect (°)	Continuous variable
Angle of shade (°) (N, NE, E, SE, S, SW, W, SW)	Continuous variable
Topological position	1=crest, 2=upper slope, 3=mid-slope, 4=lower slope, 5=floodplain, 6=gully, 7=gilgi, 8=floodplain, 9=bank, 10=prior stream, 11=levee, 12=dune crest, 13=dune slope14=swale
Grazing	1–no grazing, 2=some grazing, 3=heavy grazing, 4=roadside
Logging/Clearing	1=none, 2=some cutting/regrowth, 3=heavy cutting/cultivation
Fire	1=no sign, 2=old sign of fire, 3=recent fire
Flooding	1=no sign, 2=recent(debris present)
Landclass	1=suitable for both pasture and crop production, high fertility, minimal risk of erosion 2= Irregular cropping, moderate risk of erosion, maintain native pastures or non-destructively develop (direct drill), lower to middle slopes. 3= Suitable for permanent pasture, moderate to high erosion risk, middle to upper slopes, manage to maintain pasture stability and ground cover. 4=Usually highly erodable; leave undisturbed, steep upper slopes.
Drainage	1=poorly drained, 2=well drained, 3=rapidly drained
Soil Colour	0–5cm soil sample taken with collection of each plant pair determined using Northcote (1979)
Soil texture	0–5cm soil sample taken with collection of each plant pair determined using Northcote (1979)
Soil pH	Continuous variable
Electrical conductivity	Continuous variable
Outcrops	Absent/present
Vegetation classification - Upper stratum - Lower stratum	The dominant vegetation was recorded for each plant using a code. This code was derived from the classification system described in AUSLIG (1990). Here, the code combines the structural vegetation types described by Specht (1970) with the notation used by Beard and Webb (1974).

rainfall localities. *Austrodanthonia eriantha* occurred in localities with the lowest minimum and maximum temperatures suggesting this species is most likely to grow in cooler locations. This contrasts with *A. bipartita* and *A. fulva* which were associated with warmer localities. Seasonality of rainfall (in particular autumn and summer rainfall) was also an important determinant of species occurrence. *Austrodanthonia eriantha*, *A. caespitosa* and *A. setacea* grew in localities where summer rainfall and sunshine hours were least suggesting they may be more confined to the southern localities of the collection area. Conversely, *A. fulva* and *A. bipartita* were associated with the highest summer rainfall localities suggesting they may be more abundant in northern locations. Significant numeric environmental variables associated with *Austrodanthonia* species are given in Table 5.

Sites where *Austrodanthonia eriantha* grew had significantly lower levels of potassium in the A horizon than all other species (Table 5). *Austrodanthonia caespitosa* was associated with significantly higher nitrogen levels in both the A and B horizons than other species but phosphorus did not significantly influence the occurrence of this or any other species. *Austrodanthonia bipartita* and *A. fulva* appeared to be associated with the higher CEC values. Whilst the values for potassium and nitrogen represent low fertility soils, CEC values >15 meq/100g were associated with *A. caespitosa*, *A. bipartita* and *A. fulva* at some localities indicating these soils have higher mineral levels and potentially higher fertility. From these results, *A. eriantha* appears to be associated with relatively low fertility soils (phosphorus, nitrogen and organic carbon) as well as the narrowest ranges in soil pH and EC compared to other *Austrodanthonia* species (Figure 2).

Northing and the angle of shade each plant received were the most important numeric site variables to influencing species occurrence (Table 5). *Austrodanthonia bipartita* and *A. fulva* were generally recorded in the more northern locations, which is consistent with the finding that these species are associated with higher summer rainfall areas. *Austrodanthonia caespitosa*, *A. eriantha* and *A. setacea* were each associated with more southern localities. The angle of shade a plant received from both the NE and NW, and to a lesser extent the E and W, had a highly significant influence on the occurrence of a species. For example, *A. fulva* and *A. setacea* tended to occupy sites that received greater shading (larger angle) than *A. bipartita*, *A. caespitosa* and *A. eriantha*.

Topographic position was a highly significant factor in determining occurrence of *Austrodanthonia* species (Table 6). There were a possible 14 different topological positions (Table 4) though most plants (65% of plants) were collected from flat sites. *Austrodanthonia caespitosa* was different from other species in that 35% of these plants were collected from crests of hills or slopes and appear to occupy a wider

Table 5. Significant numeric environmental variables associated with occurrence of different *Austrodanthonia* species. Means (± s.e)

Locality variables		*Austrodanthonia* species				
		***A. bipartita* (n = 60)**	***A. caespitosa* (n = 139)**	***A. eriantha* (n = 14)**	***A. fulva* (n = 62)**	***A. setacea* (n = 48)**
Rainfall (mm)						
Mean annual rainfall	**	512 (10.0)	539 (6.6)	527 (20.8)	527 (9.9)	493 (11.2)
Summer rainfall	**	125 (2.9)	122 (1.9)	112 (6.0)	126 (2.8)	111 (3.2)
Autumn rainfall	***	108 (1.3)	107 (0.9)	105 (2.8)	108 (1.3)	100 (1.5)
Temperature (°C)						
Minimum	***	10.6 (0.10)	10.1 (0.07)	9.8 (0.22)	10.5 (0.10)	10.4 (0.12)
Maximum	**	24.2 (0.12)	23.8 (0.08)	23.5 (0.25)	24.1 (0.11)	23.9 (0.13)
Evapotranspiration (mm)						
Annual	*	484.6 (7.27)	500.7 (4.78)	487.5 (15.05)	490.4 (7.15)	472.3 (8.13)
Relative Humidity (%)						
9 am	**	64.1 (0.30)	65.4 (0.20)	66.2 (0.63)	64.5 (0.29)	64.8 (0.34)
3 pm	**	42.1 (0.28)	43.3 (0.19)	43.7 (0.59)	42.3 (0.28)	43.1 (0.32)
Sunshine hours	***	8.14 (0.04)	7.9 (0.02)	7.8 (0.07)	8.10 (0.04)	8.01 (0.04)
Soil chemical properties (A horizon)						
K (mg/kg)	*	438.3 (24.76)	444.2 (16.13)	262.1 (49.53)	425.7 (23.73)	403.9 (31.34)
Ca (meq/100g)	**	7.16 (0.580)	6.29 (0.331)	3.24 (1.017)	7.08 (0.487)	5.75 (0.643)
Al(meq/100g)	*	0.19 (0.047)	0.15 (0.031)	0.45 (0.094)	0.27 (0.045)	0.21 (0.059)
Total CEC	**	11.5 (0.683)	10.39 (0.445)	6.18 (1.366)	11.27 (0.654)	9.81 (0.864)
N (mg/kg)	**	0.098 (0.004)	0.103 (0.003)	0.070 (0.008)	0.097 (0.004)	0.095 (0.005)
(B horizon)						
pH ($CaCl_2$)	***	7.4 (0.160)	6.9 (0.093)	5.96 (0.287)	7.4 (0.148)	6.8 (0.180)
EC (dS/m)	***	1.56 (0.185)	0.79 (0.107)	0.50 (0.333)	1.31 (0.171)	0.88 (0.209)
Ca (meq/100g)	**	7.97 (0.623)	7.41 (0.361)	3.28 (0.121)	7.74 (0.577)	6.05 (0.703)
Mg (meq/100g)	***	5.29 (0.387)	3.54 (0.224)	3.18 (0.696)	4.66 (0.358)	3.98 (0.437)
Na (meq/100g)	**	1.57 (0.227)	0.67 (0.132)	0.95 (0.408)	1.30 (0.210)	0.92 (0.256)
Al (meq/100g)	**	0.086 (0.029)	0.074 (0.017)	0.287 (0.053)	0.078 (0.027)	0.123 (0.033)
Total CEC	***	15.67 (0.968)	12.39 (0.561)	8.27 (1.740)	14.57 (0.896)	11.79 (1.092)
N (mg/kg)	**	0.058 (0.0004)	0.066 (0.002)	0.054 (0.007)	0.052 (0.003)	0.066 (0.004)
Site variables						
Position in landscape						
Northing/1000	**	642.2 (1.23)	636.8 (0.81)	632.4 (2.56)	641.9 (1.22)	635.9 (1.38)
Slope (°)	*	0.6 (0.39)	1.7 (0.26)	1.5 (0.81)	1.26 (0.38)	0.35 (0.44)
Aspect (°)	*	18.4 (10.80)	49.7 (7.09)	69.3 (22.36)	35.11 (10.62)	20.0 (12.07)
Angle of shade						
NE	***	22.2 (3.40)	20.9 (2.24)	20.3 (7.05)	39.9 (3.35)	31.4 (3.80)
E	**	22.4 (2.97)	15.0 (1.95)	13.0 (6.15)	26.4 (2.92)	26.18 (3.32)
W	*	24.3 (3.33)	23.4 (2.19)	27.6 (6.91)	36.8(3.28)	24.9 (3.73)
NW	***	35.1 (3.63)	21.3 (2.39)	15.9 (7.52)	40.0 (3.57)	39.2 (4.06)

* P<0.05; ** P<0.01; *** P<0.001; ****P<0.0001

range of topological positions than other *Austrodanthonia* species. For *Austrodanthonia setacea* 27% of plants were collected on a floodplain mostly from the one locality (population 'Euabalong' on the Lachlan River), and may indicate the importance of flooding to this species. Apart from this relationship, the influences of disturbance factors such as logging, flooding and grazing were difficult to assess. A total of 79% of *A. caespitosa* plants collected were collected from disturbed areas or where there had been some grazing. This contrasts with *A. fulva* and *A. bipartita* where almost 50% of the plants were collected from areas with least obvious signs of grazing.

Whilst soil characteristics such as drainage, texture and colour appeared to be important determinants of species occurrence, clear trends were not evident. *Austrodanthonia caespitosa* was collected from all nine soil texture classes suggesting a broad adaptation compared to *A. eriantha,* which was confined largely to finer-textured soils.

The lower stratum of vegetation was important in determining species occurrence (Table 6). *Austrodanthonia caespitosa* occupied the widest range of understorey vegetation and was also the only species to be associated with weedy annual species such as *Asteraceae* (daisies). *Austrodanthonia caespitosa* was also associated with the broadest range of floristic growth forms (herbaceous plants, tufted grasses and low shrubs) compared to other *Austrodanthonia* spp. that tended to grow only with herbaceous and grassy understoreys.

All geological variables were significantly associated with species, indicating the importance of underlying geology (Table 6). *Austrodanthonia caespitosa* was associated with the widest range of lithology, the majority of plants being associated with alluvium, quartz and slate but also with igneous rocks such as basalt and rhyolite.

Most important environmental characteristics

The stepwise generalised linear models (GLM) (Table 7) suggest that autumn rainfall is an important factor in determining the occurrence of *Austrodanthonia bipartita*, *A. caespitosa* and *A. setacea*. The significance of evaporation rates over the autumn months for four out of the five species further highlights the importance of climatic conditions at this time of year. The influence of mean annual rainfall on species occurrence was confirmed by the PCA where together the first three principal components accounted for more than 95% of the variation in rainfall (Table 8). The importance of autumn rainfall is also illustrated by the high weighting of April rainfall in each of three principal components. There was no marked clustering in the principle components analyses.

As the PCA (rainfall and other climate variables) seemed to indicate that 'dryness' was associated with *Austrodanthonia caespitosa* (Table 8), the relationships between species occurrence and PC1 and PC2 for either plants that had a greater angle of shade > 45° (shaded) or angle of shade < 45° (unshaded) was further examined. Here, two patterns

Table 6. Significant factor environmental variables associated with occurrence of five *Austrodanthonia* species.

Factor variable	χ^2 value	Level of significance
Position in landscape		
– topological position	108.1	***
Disturbance		
– Logging/clearing	53.1	***
– Flooding	31.7	***
– Grazing	32.2	*
Soils		
– Drainage	31.5	***
– Texture	105.6	***
– Colour	195.2	**
– Landclass	24.9	*
– Rocky outcrops	12.3	*
Vegetation		
– Composition (lower stratum)	86.7	***
– Growth form (lower stratum)	47.3	***
– Composition (upper stratum)	35.5	*
– Growth form (upper stratum)	47.0	*
– Cover (upper stratum)	52.9	*
Geology		
– Lithology	155.1	***
– Class/texture	53.7	***
– Class	53.1	***
– Texture	22.2	***
– Period	38.9	*

* P<0.05; ** P<0.01; *** P<0.001

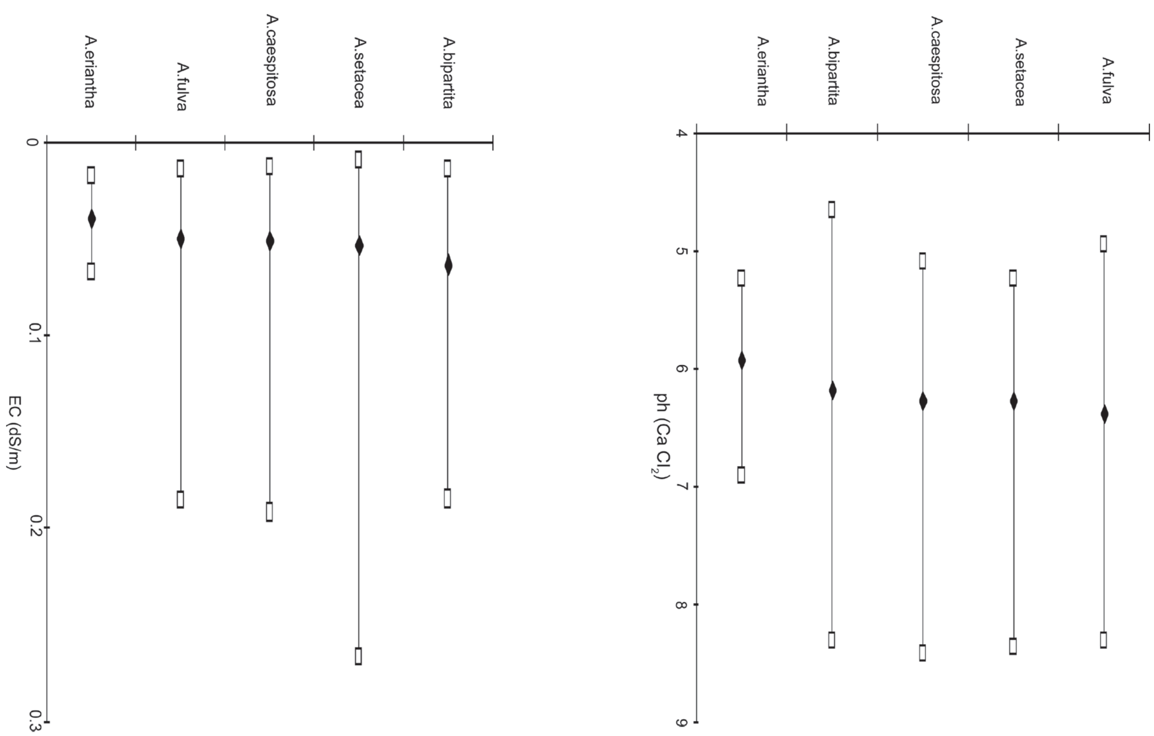

Fig. 2. The range in soil pH ($CaCl_2$) and EC (dS/m) for the soil surface samples (0–5 cm) taken with each plant for each species of *Austrodanthonia* collected. Mean values indicated by ♦, maximum and minimum values by □.

Table 7 Significant environmental variables (P<0.05) and regression coefficients (s.e) associated with occurrence of different *Austrodanthonia* species based on multiple generalised linear models with terms fitted in stepwise manner. *P<0.05; ** P<0.01; *** P<0.001; ****P<0.0001: [1]Regression coefficients shown in Appendix 1

Species	Rainfall			Climate			Site		
A. bipartita	Autumn rainfall	***	-0.14 (0.032)	Sunshine hours (Oct)	***	3.58 (1.063)	Floristic growth form (lower stratum)	***	[1]
	August rainfall	*	0.14 (0.039)	Rh 3.00pm	*	0.25 (0.111)	Northing	***	8.69 (0.00002)
	Summer rainfall	*	-0.03 (0.015)						
A. caespitosa	April rainfall	***	0.08 (0.023)	Et April	****	-0.18 (0.086)	Soil colour	***	[1]
				Sunshine hours (Oct)	***	0.53 (0.118)	Angle of shade (NW)	**	-0.17 (0.005)
				Et Autumn	**	-1.95 (0.535)	Angle of shade (E)	**	-0.01 (0.006)
							Slope	*	0.13 (0.064)
A. eriantha				Sunshine hours (Oct)	***	-5.08 (1.570)	Soil texture	****	[1]
				Rh 3.00 June	*	-0.64 (0.276)			
				Et Autumn	*	-0.40 (0.265)			
A. fulva				Et April	***	-0.33 (0.087)	Floristic growth form (lower stratum)	***	[1]
				Et May	***	-0.41 (0.119)	Angle of shade (NE)	***	0.02 (0.005)
				Et September	*	-0.17 (0.070)	Soil texture	**	[1]
							Fire	**	0.92 (0.319)
A. setacea	Autumn rainfall	*****	-0.24 (0.057)	Et March	***	-0.10 (0.035)	Flooding	*****	0.61 (8.746)
	July rainfall	**	0.18 (0.054)				Floristic (lower stratum)	**	[1]
	March rainfall	*	0.13 (0.063)				Altitude	**	-0.003 (0.00322)

emerged. *A. bipartita* and *A. fulva* occurrence declined with increasing PC weighing (dryness) whereas the occurrence of *A. caespitosa* and *A. setacea* increased (Figure 3).

The importance of northing to the occurrence of *A. bipartita* was confirmed in the stepwise GLM (Table 7). The analyses also suggested that shading is most important for *A. caespitosa* and *A. fulva*. However again, the direction and the angle of shade was different for each species. *Austrodanthonia fulva* was associated with shading from the NE whereas *A. caespitosa* had less shading from the NW and E directions.

The PCA showed 56% of the variation in site environment variables was accounted for by PC1, 2 and 3 (Table 9), highlighting the importance of these small scale site variables. A total of 73% of the variation in A horizon soil variables was accounted for by the first three principal components.

Discussion

These data show that regional trends in climate for *Austrodanthonia* species such as *Austrodanthonia caespitosa* may be modified at a local site scale, and local distribution appears to be dominated by a number of small-scale environmental factors. The relationship between small-scale site variations in the amount of shading (angle of shade) a plant received suggests that *A. caespitosa* may occupy more exposed or drier sites than other species, not just in terms of solar radiation but also in the drying effects of wind. This small-scale site variation may override the large-scale association of *A. caespitosa* with higher mean annual rainfall.

At the small-scale, 'dryness' appears to be greatest in the summer months. This indicates *Austrodanthonia caespitosa* may have more tolerance to water stress than other *Austrodanthonia* species. More exposed sites (smaller angle of shade) appear to be associated with greater *A. caespitosa* abundance, and may also imply fewer trees and higher levels of disturbance. If the angle of shade were to reflect the level of disturbance, this and other disturbance factors were unimportant as a major determinant of species abundance. Grazing regimes are considered a major disturbance agent (Whalley 1994) and studies comparing fenced and unfenced remnant grassy woodlands have shown *Austrodanthonia* cover to increase by as much as 7.5% where grazing has been excluded (Spooner *et al*. 2002). That our study was unable to find any influence of grazing on species occurrence, may have been due to the crude measure of disturbance used in this study. Grazing was determined by presence of dung, grazed plants or pads, with no assessment of the quantity (grazing intensity) or the temporal nature of grazing regimes. Drought at the time of data collection may also have meant that most of the grazing-sensitive species had disappeared or were simply not visible. Another reason for the lack of significance of disturbance on species occurrence may have been the extent of past disturbance throughout central western New South Wales where some 85% of native vegetation has

Table 8. Weightings of climatic and rainfall variables for principal components 1, 2 and 3 (PC1, PC2 & PC3) respectively, and the cumulative proportion of variation accounted for by each PC.

	Cumulative Proportion of variation	Climatic variables MaxT (annual)	MinT (winter)	Eta (annual)	Eta (autumn)	Eta (winter)	Rh09 (annual)	Rh09 (Winter)
PC1	0.5477	-0.442	-0.480	0.431	0.338	0.159	0.456	0.204
PC2	0.7532	-0.148		-0.317	-0.529	0.300	0.135	0.700
PC3	0.8860			0.126		0.904	-0.291	-0.285

		Rainfall variables Annual	Summer	March	April	Total Autumn	August
PC1	0.7708	-0.454	-0.387	-0.389	-0.368	-0.449	-0.395
PC2	0.9255		0.503	0.472	-0.547		-0.470
PC3	0.9522	0.386			-0.650	-0.284	0.586

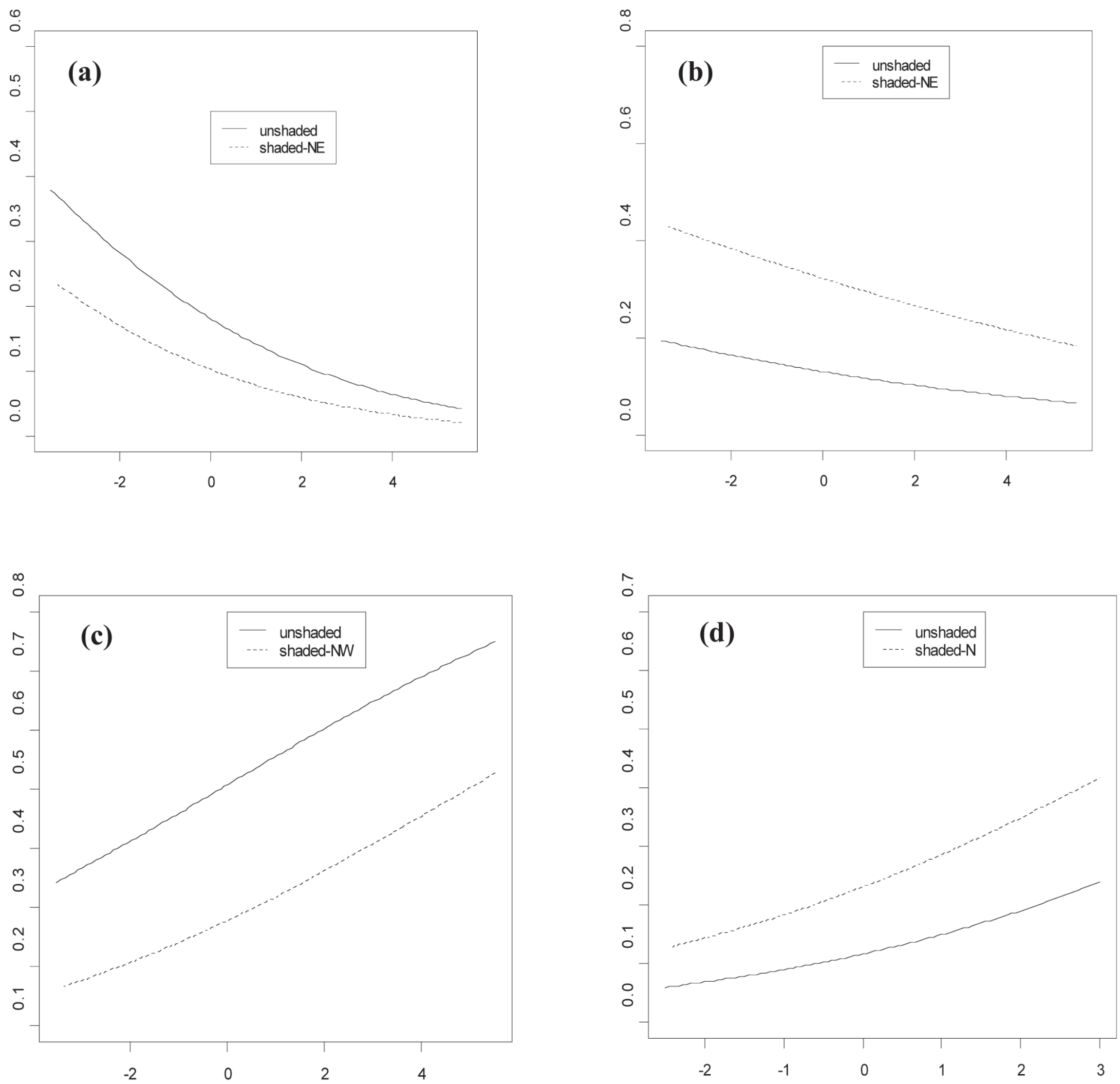

Fig. 3. Relationships between first and second principal components for climate (PC1 and PC2 respectively) and significant shading (angle of shading > 45°) from NE, NW and N directions and unshaded (angle of shading < 45°) for *Austrodanthonia bipartita* **(a)** *A. fulva* (b), *A. caespitosa* **(c)** and *A. setacea* **(d)**.

been cleared since European settlement (NSW State of the Environment Report 2006).

Austrodanthonia caespitosa occupied the widest range of understorey vegetation and was also the only species to be associated with ruderal species such as species of *Asteraceae* (daisies). Whilst disturbance factors (grazing) were not highly significant in species occurrence it may be that *A. caespitosa* has some affinity to highly disturbed sites. *Austrodanthonia caespitosa* was also associated with the broadest range of floristic growth forms (herbaceous plants, tufted grasses and low shrubs) compared to other *Austrodanthonia* species, which tended to grow only with herbaceous and grassy understories. Vegetation, however was not a major site variable in determining the occurrence of *A. caespitosa* (Table 10), although a more detailed vegetation assessment of the site environments may have revealed something different. Nevertheless, 79% of *A. caespitosa* plants were collected from disturbed areas or where there had been some grazing. This contrasts with *A. fulva* and *A. bipartita* where almost half the plants were collected from areas with least grazing and least obvious signs of grazing, and suggests that *A. caespitosa* is more tolerant of grazing and/or is a colonising species. The ability of *A. caespitosa* to colonise readily has been reported in recent studies (Waters *et al*. 2005; Hackney *et al*. 2006; Jessop & Giddings 2006).

From the univariate analyses, soil chemical properties of the B horizon had a greater influence on the abundance of species than those of the A horizon (Table 5). This may result from the movement of more mobile nutrients such as nitrogen potassium through the soil profile. However, the only variable in the B horizon that did not influence the abundance of different species was potassium.

These results demonstrate a trend for *Austrodanthonia caespitosa* to decline as pH increases, as reported by Dowling *et al*. (1996) for the NSW Southern Tablelands. Dowling *et al*. (1996) also suggested that *Austrodanthonia setacea* grew only on soils of low pH; however, this study shows *A. setacea* grows in a much broader soil pH range, with some sites being alkaline (pH >8). From this study, *Austrodanthonia eriantha* appears to be associated with low fertility soils (as measured by phosphorus, nitrogen and organic carbon) as well as the narrowest ranges in soil pH and EC. Landholders in southern NSW have reported the responsiveness of *Austrodanthonia*–based pastures to previous fertilizer application (Graham *et al*. 1998; Dalglish 1993). Scott and Whalley (1984) demonstrated populations of *Austrodanthonia* growing on high fertility sheep camp sites to be morphologically distinct from those growing peripheral to camp sites. It appears that *A. eriantha* may not be as responsive to increases in fertility as *A. caespitosa* and other closely related species.

The broader range of edaphic factors associated with *Austrodanthonia caespitosa* was also reflected in the importance of soil texture and geology. *Austrodanthonia caespitosa* was collected from all nine soil texture classes suggesting a broader adaptation compared to *A. eriantha*

Table 9. Weightings of site environment and soil chemical variables for principal components 1, 2 and 3 (PC1, PC2 and PC3) respectively, and the cumulative proportion of variation accounted for by each PC.

	Proportion of variation	Slope	Aspect	Angle of shade						Position	Grazing	Logging	Fire	Flooding	Land class	Drainage	Soil Depth	Outcrops
				N	NE	E	S	SW	W									
PC1	0.2549	.173	.140	-.274	-.365	-.359	-.367	-.386	-.322	-.253			-.133	-.212	-.226	-.190		
PC2	0.4611	-.408	-.436			-.152				.337	.297	-.104			-.190	-.320	.210	.457
PC3	0.5657	.114			-.231	-.231	0.172	0.121	0.275	-.138	.149		.391	-.555	.137	.254	.379	.136
A horizon		**pH**	**EC**	**P**	**S**	**OC**	**Ca**	**Mg**	**K**	**Al**	**CEC**	**N**						
PC1	0.4217	-.297	-.274	-.220	-.136	-.194	-.422	-.293	-.342	-.275	-.438	-.288						
PC2	0.6121	.433		-.228	-.411	-.525		0.221		-.287	.114	-.413						
PC3	0.7308	.149	-.598	-.114	-.494	0.347	0.233	-.120	-.203			.347						

Table 10. Important large-scale (regional) and small-scale (site) environmental characters associated with the occurrence of *Austrodanthonia* species.

	A. bipartita	*A. caespitosa*	*A. eriantha*	*A. fulva*	*A. setacea*
Regional environmental characters					
Rainfall	✓				
– Summer					
– Autumn	✓				✓
– April		✓			
– March					✓
– July					✓
– August	✓				
Sunshine hours (October)	✓	✓	✓		
Evaporation					
– Autumn		✓	✓		
– March					✓
– April		✓		✓	
– May				✓	
– September				✓	
Relative humidity					
– 3.00 pm (annual)	✓				
– 3.00 pm (June)			✓		
Northing	✓				
Altitude					✓
Site environmental characters					
Vegetation (lower stratum)	✓			✓	✓
Soil colour		✓			
Soil texture					
Soil class.texture[1.]	✓		✓	✓	
pH			✓		
EC		✓			
Na (A horizon)					✓
N (A horizon)			✓		
Lithology	✓	✓			
Slope					
Angle of shade – direction					
– NW		✓			
– NE				✓	
– E		✓			
Fire				✓	
Flooding					✓

[1.] Classification derived by combining dominant lithology with estimated clay content.

which was confined largely to finer-textured soils. *Austrodanthonia caespitosa* was also associated with the widest range of lithology.

The widespread co-occurrence of *Austrodanthonia* species has implications for wild-land seed harvesting as seedlots will most likely contain a range of species. The weightings in the PCA suggest that there was not an exclusive set of environmental variables associated with the occurrence of different species and wild-land harvested *Austrodanthonia* seed is likely to contain material suited to a range of environments. Where the re-seeding objective is for rehabilitation or re-introduction of native pastures, this wild-land harvested seed may have advantages.

Whilst *Austrodanthonia caespitosa* occurs widely across the study area, it was difficult to collect plants of *Austrodanthonia* in the central and southern portions of the collection area, where eight localities contained no *Austrodanthonia*. Five of these southern locations were south-east of West Wyalong. The initial plant collection spanned some six months (late autumn to early spring) and these southern localities were revisited in November and December 2003 to re-attempt collection. However no *Austrodanthonia* was found on these subsequent visits despite the Australian National Herbarium recording *A. caespitosa*, *A. eriantha* and *A. setacea* as being widespread throughout the area (Australian Virtual Herbarium 2007). It is possible that populations from these localities experience a flowering period later than December (D. Garden *pers. comm.*), despite reports by Hodgkinson and

Quinn (1978) of predominately spring flowering populations growing in these areas. Whilst some vegetative plants were collected from localities on the western margin of the collection area, no grasses resembling *Austrodanthonia* were found in these southern localities probably due to the protracted drought within the area.

The transplants of two populations, Caragabal (locality 33) and Cowra (locality 35) failed to produce viable seed, and those from Peak Hill (locality 16) and Cumnock (locality 23) produced only small quantities of seed. These localities did not share any common features and, as most plants in each population were flowering or had mature inflorescences at the time of collection, these may have been unviable field hybrids akin to the plants with atypical chromosome number and meiosis reported by Brock and Brown (1961). Non-flowering individuals of *A. eriantha* and *A. bipartita* have also been reported in the studies of O'Dwyer and Attiwill (2000) and Lodge (1981) respectively.

As *Austrodanthonia fulva* and *A. bipartita* are associated with the highest summer rainfall localities (northern locations), a greater requirement for summer rainfall for these species may help to ensure seedling survival following late spring flowering. It follows that these species may have a dominant spring flowering. The association for *A. caespitosa* with higher rainfall and/or reduced evapotranspiration rates in autumn may reduce the risk of seedling mortality as plants enter a time of year where moisture stress is becoming increasingly less likely. The significant positive regression coefficient of April rainfall for *A. caespitosa* suggests this species could have some capacity for autumn flowering or growth, in addition to the documented spring flowering. Cunningham *et al*. (1992) document this species as flowering predominantly in spring in western NSW, but others have reported flowering within this area to occur at any time of year in response to rainfall (Hodgkinson & Quinn 1978). So, though *A. caespitosa* is considered a spring-flowering species, our data suggests that autumn flowering is at least of equal importance.

For *Austrodanthonia bipartita* and *A. setacea* the negative autumn rainfall regression coefficient suggests less growth and/or flowering in autumn. *Austrodanthonia bipartita* has been reported to flower in spring and autumn (Lodge 1983 as cited in Lodge 1993; Cunningham *et al*. 1992) and autumn establishment of *Austrodanthonia* species on the NSW North West Slopes (Lodge 1981) has also been reported. Autumn flowering/establishment may have the added advantages of higher mean minimum temperature and less temperature fluctuation than those in spring (Lodge 1981). *A. setacea* is generally considered a spring-flowering species (Cunningham *et al*. 1992) and this may be reflected in the positive regression coefficient of July rainfall in this study.

A. eriantha and *A. caespitosa* were associated with locations that received the least number of sunshine hours so it would be expected that these species would be more abundant in the southern sites of the collection area. Conversely, *A. bipartita* and *A. fulva* were both associated with locations that received the most sunshine hours and would be expected to occupy more northerly sites. For *A. bipartita*, *A. caespitosa* and *A. eriantha* the number of sunshine hours in October was a major indicator of potential occurrence.

Conclusions

Numerous ecological factors (both large and small-scale) allow *Austrodanthonia* species to co-exist (summarised in Table 10). However, *Austrodanthonia caespitosa* appears to cover a broader range of environments than other closely related-species, explaining the widespread occurrence of this species in central western New South Wales and other areas in Australia. Large-scale rainfall and climatic factors had a major correlation with the abundance of different species. The importance of higher autumn rainfall for *Austrodanthonia bipartita*, *A. caespitosa* and *A. setacea* suggest that flowering and seasonality of growth may be determinate in nature for these species and not the case for other species. Numerous smaller-scale environmental factors are important in determining the local abundance of species. It appears that regional rainfall and climate influences on species abundance are modified at a local site scale depending on exposure to solar radiation. Vegetation (of the lower strata) is important for three species *A. bipartita*, *A fulva* and *A. setacea*, but unimportant to *A. caespitosa*. Whether this indicates *A. caespitosa* has a greater adaptive potential than related species may possibly be explored by examining morphological characteristics between populations.

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Appendix 1. Regression coefficients (standard errors) from multiple generalised linear models examining the relationship site environmental variables and occurrence of five species of *Austrodanthonia*.

		A. bipartita	*A. caespitosa*	*A. eriantha*	*A. fulva*	*A. setacea*
Soil Colour[1]	10R4/8		1.14 (1.27)			
	10Y3/2		-15.5 (3.95)			
	10YR4/2		-1.34 (1.58)			
	10YR4/3		1.10 (1.69)			
	10YR4/4		0.46 (1.38)			
	10YR4/6		18.5 (2.79)			
	10YR5/2		-16.6 (3.95)			
	10YR5/3		1.97 (1.41)			
	10YR5/4		0.90 (1.31)			
	10YR6/3		16.8 (3.95)			
	2.5Y4/4		-.94 (1.61)			
	2.5Y5/4		17.8 (3.95)			
	2.5Y3/3		-18.8 (3.95)			
	2.5YR3/4		1.3 (1.22)			
	2.5YR3/6		0.8 (1.16)			
	2.5YR4/4		-0.3 (2.07			
	2.5YR4/6		1.6 (1.20)			
	2.5YR4/8		0.5 (1.23)			
	5YR3/3		0.8 (1.52)			
	5YR3/4		-16.3 (1.81)			
	5YR4/3		16.9 (2.28)			
	5YR4/4		0.19 (1.26)			
	5YR4/6		1.7 (1.19)			
	5YR5/2		-0.1 (1.54)			
	5YR5/3		-14.8 (2.79)			
	5YR5/6		-16.7 (2.79)			
	7.5YR3/4		0.7 (1.53)			
	7.5YR4/6		18.4 (2.79)			
	7.5YR5/3		-1.0 (1.62)			
	7.5YR5/4		0.01 (1.42)			
Vegetation	Tussock or tufted grasses	-2.3 (3.54)				
	Tall Shrubs understorey	1.3 (7.57)				
	Asteraceae understorey	-2.86 (1.08)			1.7 (2.32)	-17.4 (1.09)
	Graminoids understorey				18.2 (1.51)	-0.7 (1.31)
	Mixed understorey				17.9 (1.51)	-2.3 (1.12)
	Other grasses understorey				18.7 (1.51)	-2.6 (1.15)
Soil texture[1]	Clay sand			1.9 (0.16)	-16.6 (1.94)	
	Clay sandy loam			3.5 (0.80)	0.66 (0.96)	
	Loam			1.8 (0.16)	-1.2 (0.48)	
	Loam clay			3.4 (0.30)	0.1 (0.48)	
	Medium clay			3.4 (0.50)	0.3 (1.21)	
	Loam sand			1.6 (0.16)	-16.7 (2.43)	
	Sandy clay loam			3.5 (0.68)	-18.1 (2.35)	
	Sandy loam			1.8 (0.16)	-0.4 (5.43)	

[1] According to Northcote (1979)