CHAPTER SEVEN

Environmental determinants of ground-storey composition

Private remnant vegetation north of Armidale, Northern Tablelands, NSW

7.1 INTRODUCTION

Environmental variables, like management variables (as discussed in Chapter 6), are important determinants of composition including ground-storey vegetation (Australian State of the Environment Committee 2001). The environment shapes vegetation at both a local and landscape scale (Kent and Coker 1992). Vegetation compositional studies are generally of two types: the relationship of composition to many environmental variables (e.g. McIntyre and Lavorel 1994a; Lunt 1997; McIntyre and Martin 2001; Clarke 2003), or to a restricted number of environmental variables such as aspect and parent material, as studied by Bean and Whalley (2001).

Many environmental variables in relation to grassy vegetation have been studied in Australia: lithology and related soil types (e.g. Prober and Thiele 1995; Lunt 1997; Bean and Whalley 2001; Prober *et al.* 2002a; Prober *et al.* 2002b), tree influence (Chilcott *et al.* 1997; Gibbs *et al.* 1999; Prober *et al.* 2002a), and climatic influences (Harris and Lazenby 1974; Walker *et al.* 1996). Other components such as aspect, altitude, geographical position and landscape morphological position have not been as thoroughly researched, but have been included as covariables in studies investigating management influences (e.g. McIntyre and Lavorel 1994; Prober and Thiele 1995; Clarke 2003).

Given the importance of environmental variables in determining ground-storey species composition, this chapter aims to establish which environmental variables significantly affect the composition of ground-storey vegetation, and their influence on ground-storey composition in grazed production systems on the Northern Tablelands of NSW. The effects of environmental variables on species composition were addressed by:

1. identifying which environmental variables affect ground-storey composition on the Northern Tablelands by partitioning the variance in the regional site x species data set among the explanatory environmental variables; and
2. investigating how plant species are affected by important environmental variables.

7.2 METHODS

7.2.1 Sampling and analysis

Sampling and analytical methods were described in Chapters 4 and 6. The environmental variables measured were described in Chapter 4. There are four main categories, namely sampling date and geographical, soil and climatic variables (Figure 7.1).

7.3 RESULTS

Environmental variables accounted for 61% of the explained variance in the reduced data set in the Canonical Correspondence Analysis (CCA) of the regional ground-storey flora (Figure 7.2).

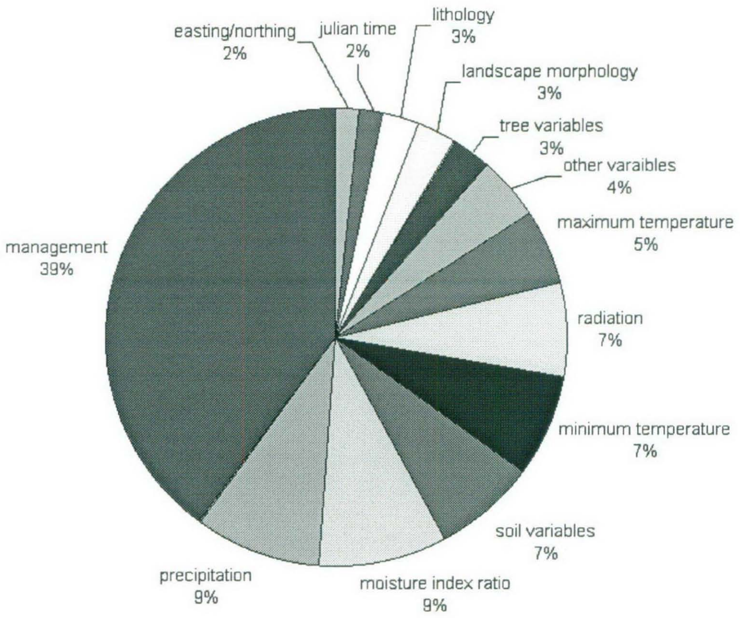

Figure 7.2 Percentages of explained variance attributed to various environmental variables in the analysis of the regional ground-storey flora data set with CCA. The variance attributed to management variables is included for comparison (see Chapter 6).

Environmental Variables

Soil nutrients:
- Total nitrogen
- Sulphur
- Phosphorus (Colwell)
- Organic carbon
- pH (1:5 $CaCl_2$)
- pH (1:5 water)
- Bulk density

Sampling Date:
- Julian time

Geographical variables:
- Lithology
    - Basalt
    - Metasediment
    - Granite
- Geographical position
    - North-south
    - East-west
- Altitude
- Slope
- Aspect
- Position in landscape
    - Accumulating water
    - Shedding water
- Tree presence
- Percentage of site under tree canopy
- Landscape morphology
    - Valley bottom
    - Flat
    - Lower slope
    - Mid slope
    - Upper slope
    - Ridge top

Climate variables:
- Minimum temperature
    - Mean annual
    - Absolute minimum
    - Monthly average
    - Winter average
    - Summer average
- Maximum temperature
    - Mean annual
    - Absolute maximum
    - Monthly average
    - Winter average
    - Summer average
- Radiation
    - Mean annual
    - Monthly average
    - Winter average
    - Summer average
- Precipitation
    - Mean annual
    - Monthly average
    - Winter average
    - Summer average
- Moisture index
    - Mean annual
    - Monthly average
    - Winter average
    - Summer average

Figure 7.1 Environmental variables used in the analysis of the regional ground-storey flora data set. These variables are defined in Section 4.2.4.

7.3.1 Soil nutrients

Soil nutrient variables accounted for 7% of the explained variance with the variance being partitioned between total nitrogen (3.3%), pH_{Ca} (1.1%), sulphur (0.9%), phosphorus (0.9%) and organic carbon (0.9%). Bulk density and pH_{H2O} were not significant and were removed in the second forward selection analysis. All other soil variables were significant (Table 7.1) and are shown as vectors in the site ordination plot (Figure 7.3). All point upwards and therefore are positively aligned with axis 2 (Section 4.3.4).

Table 7.1 All forward selection results of soil analysis variables in the CCA. Non-significant ($p > 0.05$) variables removed in the reduction of the data set after the first forward selection analysis are indicated by ^{z}. Sorted by ascending values of p.

Soil nutrient variable	F	p
pH_{Ca}	1.87	0.002
Phosphorus	1.62	0.002
Total nitrogen	4.99	0.002
Organic carbon	1.43	0.002
Sulphur	1.53	0.006
pH_{H2O}	1.18	0.082^z
Bulk density	1.08	0.256^z

The phosphorus and nitrogen vectors in the biplot are almost identical and highly correlated, and therefore floristic interpretation of the results for nitrogen are equally applicable for phosphorus. The influence of other soil nutrients on botanical composition is summarised in Appendix 7.1. Five of the ten species associated with high phosphorus and nitrogen levels were exotic (Table 7.2, Figure 7.4). The native species, *Einadia nutans* subsp. *nutans, Chenopodium pumilio* and *Convolvulus erubescens,* and the exotics, *Bromus cartharticus* and *B. brevis,* occurred mainly at sites with high soil levels of available phosphorus (Colwell) and total nitrogen. Conversely the natives, *Aristida calycina* var. *calycina, A. jerichoensis* var. *subspinulifera, A. vagans* and *Cheilanthes sieberi* subsp. *sieberi,* were associated with low levels of these macronutrients.

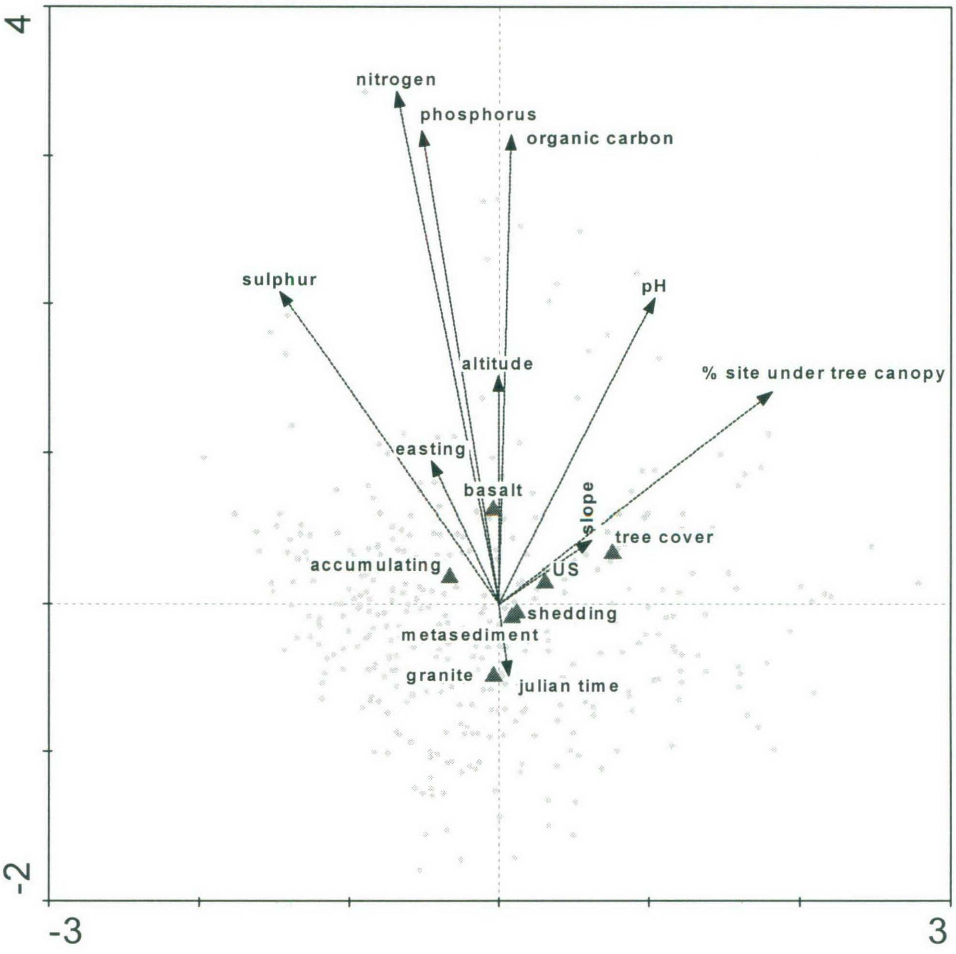

Figure 7.3 Ordination biplot from CCA illustrating only the significant environmental variables (excluding climate variables). Sites, ●; nominal environmental variables, ▲; continuous or scaler environmental variables represented by vectors. Label: US, upper slope. Slope label vertical due to lack of space for horizontal label.

Table 7.2 Species with the largest positive and negative associations with the vector of increasing soil nitrogen and phosphorus in the species ordination biplot (Figure 7.4). Species frequencies calculated from n = 373 sites. Sorted by descending frequency.

Positive relationship with high soil nitrogen and phosphorus	Frequency (%)	Negative relationship with high soil nitrogen and phosphorus	Frequency (%)
Austrodanthonia bipartita	7	**Setaria gracilis*	11
**Taraxacum officinale*	7	*Cheilanthes sieberi* subsp. *sieberi*	9
**Medicago laciniata*	6	*Aristida vagans*	4
**Modiola caroliniana*	6	*Cymbopogon refractus*	4
Polygonum aviculare	5	**Schkuhria pinnata* var. *abrotanoides*	4
Einadia nutans subsp. *nutans*	3	*Hibbertia obtusifolia*	3
**Bromus cartharticus*	3	*Solenogyne bellioides*	3
**Bromus brevis*	3	*Aristida calycina* var. *calycina*	2
Chenopodium pumilio	2	*Aristida jerichoensis* var. *subspinulifera*	2
Convolvulus erubescens	2	*Wahlenbergia stricta* subsp. *stricta*	2

* Exotic species

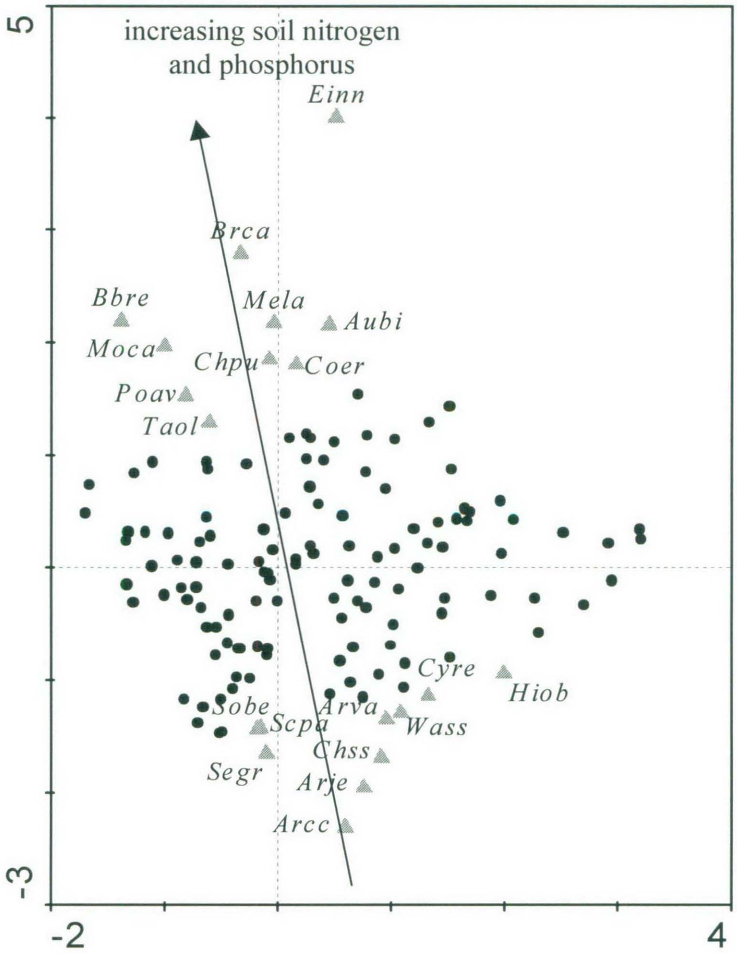

Figure 7.4 Species ordination biplot from CCA illustrating the ten species with the largest positive and negative associations with the vector of increasing soil nitrogen and phosphorus. Unidentified species, •; identified species, ▲; soil nitrogen and phosphorus represented by vector. Species codes: *Arcc – Aristida calycina* var. *calycina, Arje – Aristida jerichoensis* var. *subspinulifera, Aubi – Austrodanthonia bipartita, Arva – Aristida vagans, Bbre – Bromus brevis, Brca – Bromus cartharticus, Chss – Cheilanthes sieberi* subsp. *sieberi, Chpu – Chenopodium pumilio, Coer – Convolvulus erubescens, Cyre – Cymbopogon refractus, Einn – Einadia nutans* subsp. *nutans, Hiob – Hibbertia obtusifolia, Mela – Medicago laciniata, Moca – Modiola caroliniana, Poav – Polygonum aviculare, Scpa – Schkuhria pinnata* var. *abrotanoides, Segr – Setaria gracilis, Sobe – Solenogyne bellioides, Taol – Taraxacum officinale, Wass – Wahlenbergia stricta* subsp. *stricta.*

7.3.2 Geographical variables and Julian time

Geographical variables and Julian time accounted for 14.2% and 1.6% of the explained variance, respectively (Figure 7.2). Summaries of the influence of significant geographical variables (with the exception of increasing tree cover) and Julian time on botanical composition are given in Appendix 7.2. Five of the six landscape morphology types (Table

4.29) from valley bottom to ridge top were not significant in the first forward selection analysis. The exception was upper slope (p = 0.002). The other landscape morphology elements were retained in the analysis due to their dependence on one another (Table 7.3). Landscape morphological type accounted for only 3% of the explained variance (Figure 7.2). Upper slope was located near the centre of the site ordination plot in the upper right quadrant (Figure 7.3). Not surprisingly, it was closely aligned with slope.

Lithology significantly affected species composition (p = 0.002), explaining 3% of the explained variance. The granite centroid was located more or less directly on axis 2 at a value of –0.6, metasediment was close to the origin in the centre of the ordination, and the basalt centroid was located on axis 2 at a value of 0.6, opposite granite. The different lithologies were sampled in the ratios, 1.3 granite : 1.0 metasediment : 1.1 basalt. The native grasses, *Elymus scaber* var. *scaber, Austrodanthonia racemosa* var. *racemosa* and *Microlaena stipoides*, and the exotic annuals, *Conyza albida* and *Plantago lanceolata,* were associated with the basalt centroid (Figure 5, Appendix 7.2). Metasediments were associated with the native grasses, *E. scaber* var. *scaber* and *M. stipoides*, and the herbs, *Hypochaeris glabra/radicata, Euchiton sphaericum, Carex inversa* and *Oxalis exilis. H. glabra/radicata* and *E. sphaericum* were also associated with granite, as were the native grasses *Sporobolus creber* and *Panicum effusum* (Figures 6 and 7, Appendix 7.2).

In terms of geographical position, only geographical position east-west was significant in determining species composition (p = 0.002). Geographical position accounted for 1.6% of the explained variance. The geographical position east-west vector projected into the upper left quadrant of the ordination, associated with the exotic grasses, *Phalaris aquatica, Bromus brevis* and *B. cartharticus*, and exotic herbs, *Medicago laciniata, Modiola caroliniana* and *Polygonum aviculare* (Figure 1, Appendix 7.2).

Altitude and slope were significant influences of species composition (p = 0.008 and p = 0.026 respectively) and run-on was marginally significant (p = 0.058). Altitude was closely aligned with axis 2. The slope vector projected into the upper right quadrant of the site ordination diagram (Figure 7.3), whereas the run-on centroid was located in the upper left quadrant. Increasing slope was associated with the native herbs, *Poranthera microphylla*, *Veronica calycina* and *Dianella revoluta* var. *revoluta*, and the grasses, *Pennisetum alopecuroides, Setaria gracilis, S. pumila* and *Eragrostis molybdea* (Figure 2,

Appendix 7.2). Flat sites, (no slope) were associated with the exotic pasture grass, *Festuca pratensis,* the native grasses, *Eragrostis benthamii, E. molybdea, Cynodon dactylon, Pennisetum alopecuroides* and *Lachnagrostis aemula*, and the native pin rush, *Juncus usitatus.* Lower altitudes were associated with the forbs, *Juncus usitatus*, *Solenogyne bellioides* and *Schoenus apogon,* and the native grasses, *Aristida vagans, A. calycina* var. *calycina, A. jerichoensis* var. *subspinulifera* and *Eragrostis brownii* (Figure 3, Appendix 7.2). Exotic herbs (*Medicago laciniata, Modiola caroliniana* and *Polygonum aviculare*) and grasses (*Austrodanthonia bipartita*, *Bromus cartharticus* and *B. brevis*) were associated with increasing altitude in the study region.

Neither of the wave functions for aspect were significant (p = 0.188 and p = 0.09). The distance to travelling stock route or reserve was significant (p = 0.002) and explained 0.9% of the variance in CCA floristic associations.

The two variables associated with trees, tree presence and the percentage of site under tree canopy, were both significant (p = 0.002) in relation to species composition. Tree presence accounted for 2% of the explained variance, and the percentage of the site under tree canopy explained 1%. Both variables were located in the upper right of the site ordination (Figure 7.3), in close proximity to one another, indicating a high level of correlation between them. Species associated with increasing tree cover included *Einadia nutans* subsp. *nutans, Poranthera microphylla, Plantago debilis* and *Lomandra multiflora* subsp. *multiflora* (Table 7.4, Figure 7.5). The ten species most associated with little or no tree cover were mostly native, including *Eragrostis brownii*, *E. molybdea* and *Lachnagrostis aemula.* One exception was *Festuca pratensis,* a species generally associated with pasture improvement and therefore not present in areas with high tree cover due to absence of cultivation.

Table 7.3 All forward selection results for geographical variables and Julian time in the CCA. Non-significant ($p > 0.05$) variables not removed from the reduction of the data set (first forward selection) because they were dependent on other dummy variables are indicated by a superscript, $^{\theta}$. Cosine of aspect was not removed in the reduction of the data set after the first forward selection analysis as $p \sim 0.05$.

Geographical variables and Julian time	F	p
Lithology – granite	2.08	0.002
Lithology – metasediment	2.13	0.002
Landscape morphology – upper slope	1.49	0.002
Landscape morphology – flat	1.09	0.206^{θ}
Landscape morphology – ridge top	1.06	0.340^{θ}
Landscape morphology – lower slope	0.99	0.550^{θ}
Landscape morphology – mid slope	0.91	0.816^{θ}
Landscape morphology – valley bottom	0.76	0.966^{θ}
Geographical position – east-west	1.47	0.002
Geographical position – north-south	1.16	0.078
Cosine of aspect (result for first forward selection)	1.17	0.052
Cosine of aspect (result for second forward selection)	1.13	0.090
Sine of aspect (result for first forward selection)	1.14	0.088^{θ}
Sine of aspect (result for second forward selection)	1.10	0.188
Distance to travelling stock route	1.56	0.002
Julian time	2.56	0.002
Altitude	1.28	0.008
Slope	1.24	0.026
Position in landscape – accumulating water	1.19	0.058

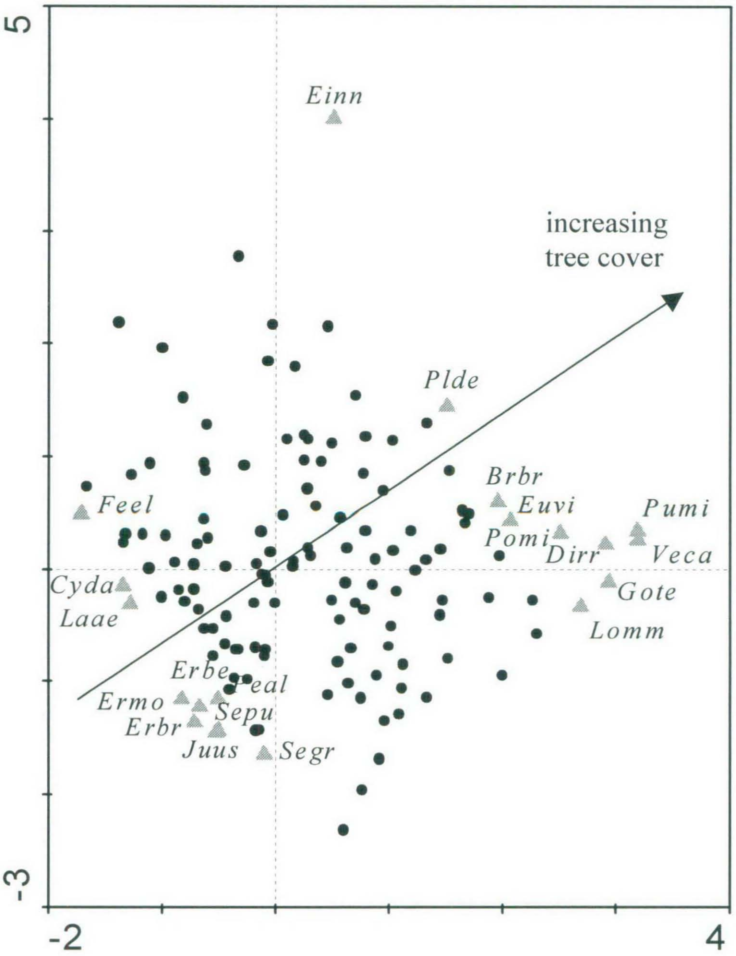

Figure 7.5 Species ordination biplot from CCA illustrating the ten species with the largest positive and negative associations with the vector of increasing tree cover. Unidentified species, •; identified species, ▲; tree cover variable represented by vector. Species codes: *Brbr – Bracteantha bracteata, Cyda – Cynodon dactylon, Einn – Einadia nutans* subsp. *nutans, Erbe – Eragrostis benthamii, Erbr – Eragrostis brownii, Ermo – Eragrostis molybdea, Euvi – Eucalyptus viminalis, Feel – Festuca pratensis, Gote – Gonocarpus tetragynus, Juus – Juncus usitatus, Laae – Lachnagrostis aemula, Lomm – Lomandra multiflora* subsp. *multiflora, Peal – Pennisetum alopecuroides, Plde – Plantago debilis, Pomi – Poranthera microphylla, Pumi – Pultenaea microphylla, Segr – Setaria gracilis, Sepu – Setaria pumila, Veca – Veronica calycina.*

Table 7.4 Species with the largest positive and negative associations with the vector of increasing tree cover in the species ordination biplot (Figure 7.5). Species frequencies calculated from n = 373 sites. Sorted by descending frequency.

Positive relationship with high tree cover	Frequency (%)	Negative relationship with high tree cover	Frequency (%)
Dianella revoluta var. *revoluta*	3	*Cynodon dactylon*	23
Einadia nutans subsp. *nutans*	3	*Eragrostis benthamii*	13
Eucalyptus viminalis	3	*Juncus usitatus*	12
Gonocarpus tetragynus	3	**Setaria gracilis*	11
Plantago debilis	3	*Pennisetum alopecuroides*	11
Bracteantha bracteata	2	*Eragrostis brownii*	10
Lomandra multiflora subsp. *multiflora*	2	**Festuca pratensis*	8
Poranthera microphylla	2	**Setaria pumila*	6
Pultenaea microphylla	2	*Eragrostis molybdea*	4
Veronica calycina	2	*Lachnagrostis aemula*	3

* Exotic species

7.3.3 Climate variables

Temperature

Temperature was the climatic variable that accounted for most explained variance. Minimum temperature variables explained 7% and maximum temperature variables explained 5%. A total of ten temperature variables were significant: six minimum temperatures (January, May, June, July, September and Summer average) and four maximum (March, June, August and December) (Table 7.5). Lowest minimum temperature was the same as the July minimum temperature and was therefore not included.

The significant minimum and maximum temperature vectors all pointed in the same general direction in the ordination diagram (Figure 7.6). Minimum temperature for January and maximum temperatures for March and December were the strongest vectors and were closely aligned with negative values on axis 2. The species that mainly occurred in warmer sites (i.e. highest minima and maxima) included *Aristida calycina* var. *calycina, A. jerichoensis* var. *subspinulifera, Cheilanthes sieberi* subsp. *sieberi* and *Setaria gracilis*. *Einadia nutans* subsp. *nutans, Bromus cartharticus, B. brevis* and *Medicago laciniata* were all associated with cooler temperatures (i.e. lowest minima and maxima) (Figure 7.7, Table 7.6).

Table 7.5 All forward selection results of minimum and maximum temperature variables in the CCA. Non-significant ($p > 0.05$) variables removed in the reduction of the data set after the first forward selection analysis are indicated by ^{z}. Sorted by ascending values of p.

Minimum temperature variables	F	p
January minimum temperature	1.74	0.002
June minimum temperature	1.74	0.002
Summer minimum temperature	1.48	0.002
May minimum temperature	1.24	0.026
September minimum temperature	1.23	0.030
July minimum temperature	1.22	0.030
April minimum temperature	1.17	0.068
November minimum temperature	1.16	0.084
August minimum temperature	1.16	0.088^{z}
October minimum temperature	1.13	0.114
December minimum temperature	1.10	0.180^{z}
March minimum temperature	1.06	0.310^{z}
February minimum temperature	1.05	0.318^{z}
Maximum temperature variables	F	p
December maximum temperature	1.75	0.002
March maximum temperature	1.50	0.002
August maximum temperature	1.30	0.008
June maximum temperature	1.20	0.040
October maximum temperature	1.18	0.052
May maximum temperature	1.12	0.138^{z}
Winter maximum temperature	1.08	0.234
Absolute maximum temperature	1.07	0.308
Summer maximum temperature	1.06	0.322^{z}
January maximum temperature	1.06	0.338^{z}
July maximum temperature	1.03	0.398^{z}
November maximum temperature	0.99	0.554
September maximum temperature	0.90	0.752^{z}
February maximum temperature	0.91	0.800^{z}
April maximum temperature	0.89	0.890^{z}

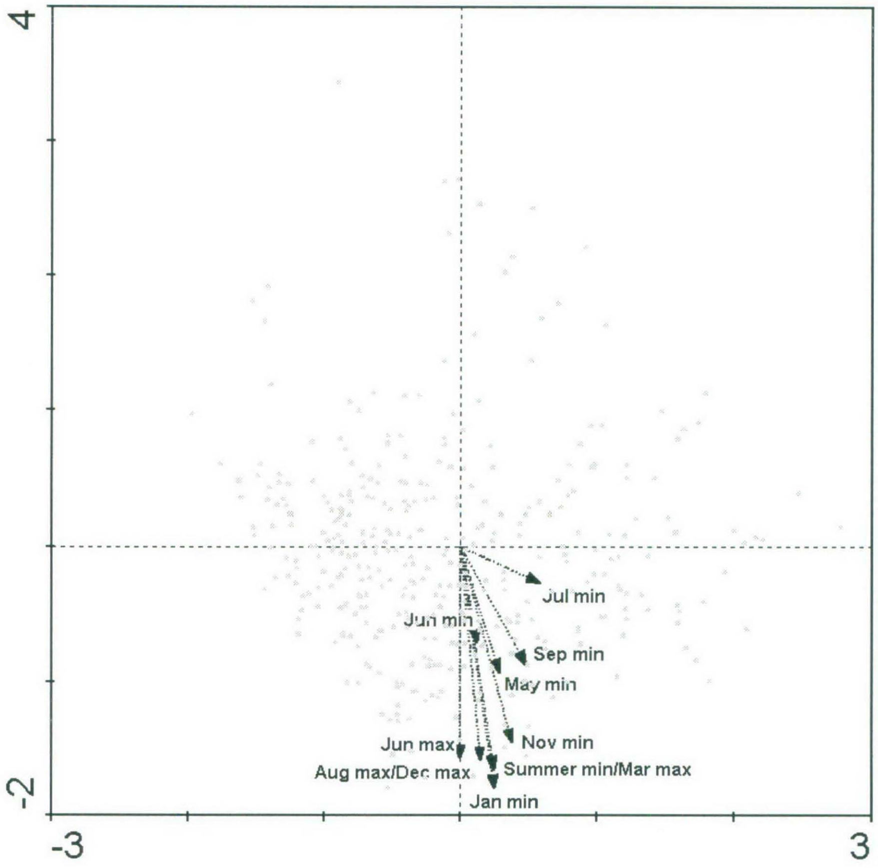

Figure 7.6 Site and temperature variables ordination biplot for CCA illustrating only significant variables. Sites represented by ●, and temperature variables represented by vectors.

Table 7.6 Species with the largest positive and negative associations with the increasing temperature vector in the species ordination biplot (Figure 7.6). Species frequencies calculated from n = 373 sites. Sorted by descending frequency.

Positive relationship with increasing temperature	Frequency (%)	Negative relationship with increasing temperature	Frequency (%)
*_Setaria gracilis_	11	_Austrodanthonia bipartita_	7
Cheilanthes sieberi subsp. _sieberi_	9	*_Medicago laciniata_	6
*_Setaria pumila_	6	*_Modiola caroliniana_	6
Aristida vagans	4	*_Polygonum aviculare_	5
Cymbopogon refractus	4	_Vittadinia cuneata_ var. _cuneata_	5
*_Schkuhria pinnata var. abrotanoides_	4	_Einadia nutans_ subsp. _nutans_	3
Solenogyne bellioides	3	*_Bromus cartharticus_	3
Aristida calycina var. _calycina_	2	*_Bromus brevis_	3
Aristida jerichoensis var. _subspinulifera_	2	_Chenopodium pumilio_	2
Wahlenbergia stricta subsp. stricta	2	_Convolvulus erubescens_	2

* Exotic species

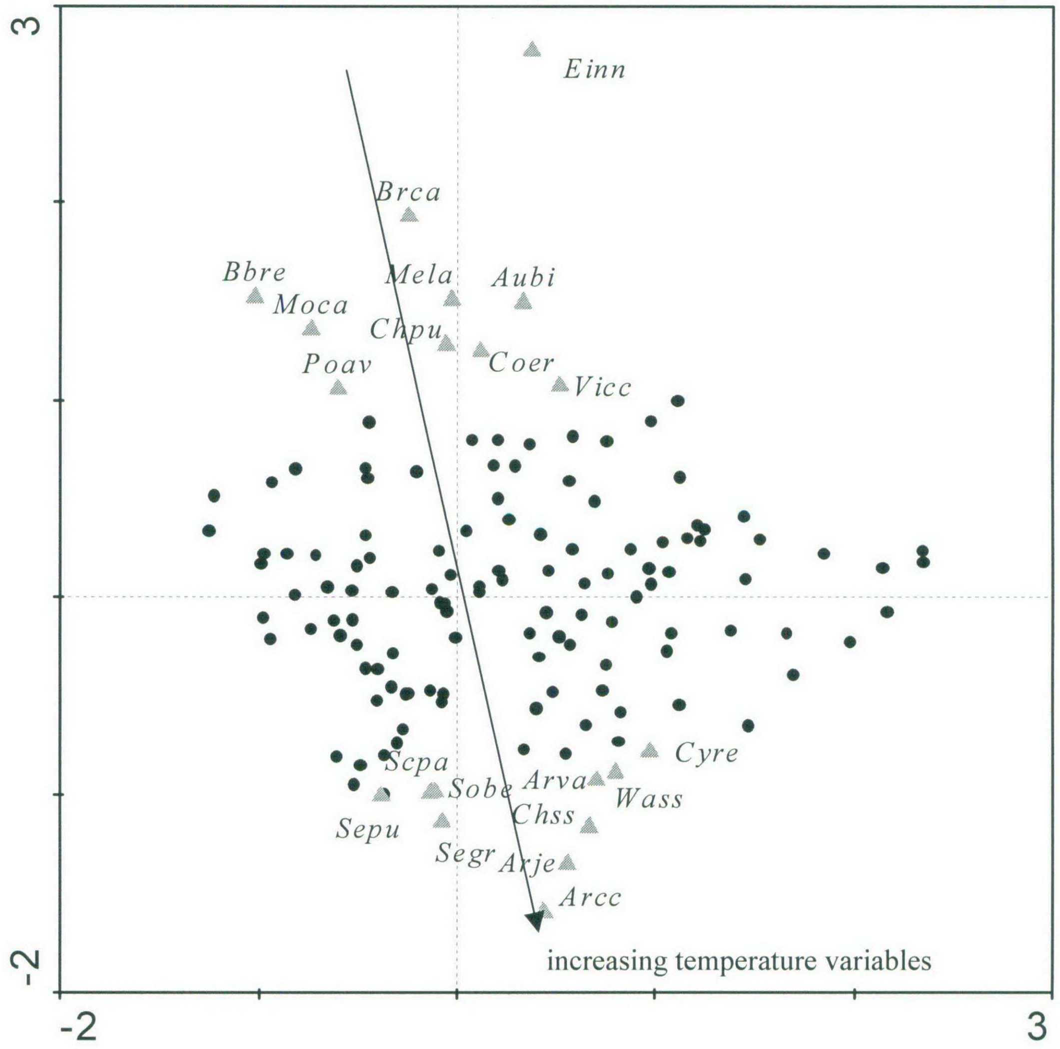

Figure 7.7 Species ordination biplot from CCA illustrating the ten species with the largest positive and negative associations with the vector of increasing temperature. Unidentified species, •; identified species, ▲; temperature variable represented by vector. Species codes: *Arcc – Aristida calycina var. calycina, Arje – Aristida jerichoensis var. subspinulifera, Arva – Aristida vagans, Aubi – Austrodanthonia bipartita, Bbre – Bromus brevis, Brca – Bromus cartharticus, Chss – Cheilanthes sieberi subsp. sieberi, Chpu – Chenopodium pumilio, Coer – Convolvulus erubescens, Cyre – Cymbopogon refractus, Einn – Einadia nutans* subsp. *nutans, Mela – Medicago laciniata, Moca – Modiola caroliniana, Poav – Polygonum aviculare, Scpa – Schkuhria pinnata var. abrotanoides, Segr – Setaria gracilis, Sepu – Setaria pumila, Sobe – Solenogyne bellioides, Vicc – Vittadinia cuneata var. cuneata, Wass – Wahlenbergia stricta subsp. stricta.*

Radiation

Radiation variables accounted for 7% of the explained variance. Six radiation variables significantly influenced species composition: May, June, July, November, December and mean annual radiation (Table 7.7). Radiation vectors were split into two seasonal groups in different sectors of the plot: winter radiation (May, June and July) in the upper right quadrat of the ordination, and summer radiation (November and December) and mean annual radiation in the lower right quadrant (Figure 7.8). Species associated with high mean solar radiation were all native and included *Pultenaea microphylla, Veronica calycina* and *Dianella revoluta* var. *revoluta*. At the opposite end of the radiation vector, all species were exotic with the exception of *Cynodon dactylon* (Table 7.8, Figure 7.9).

Table 7.7 All forward selection results for radiation variables in the CCA. Variables removed in reduction of the data set by forward selection of variables were not significant ($p > 0.05$) and are indicated by a superscript, ^{z}. Sorted by ascending values of p.

Radiation variable	F	p
June radiation	2.08	0.002
November radiation	1.81	0.002
Mean radiation	1.37	0.006
December radiation	1.31	0.006
May radiation	1.32	0.014
October radiation	1.20	0.026
July radiation	1.22	0.032
March radiation	1.19	0.058^z
February radiation	1.15	0.116^z
September radiation	1.10	0.164^z
January radiation	1.11	0.190^z
April radiation	1.08	0.240^z
August radiation	1.07	0.288^z

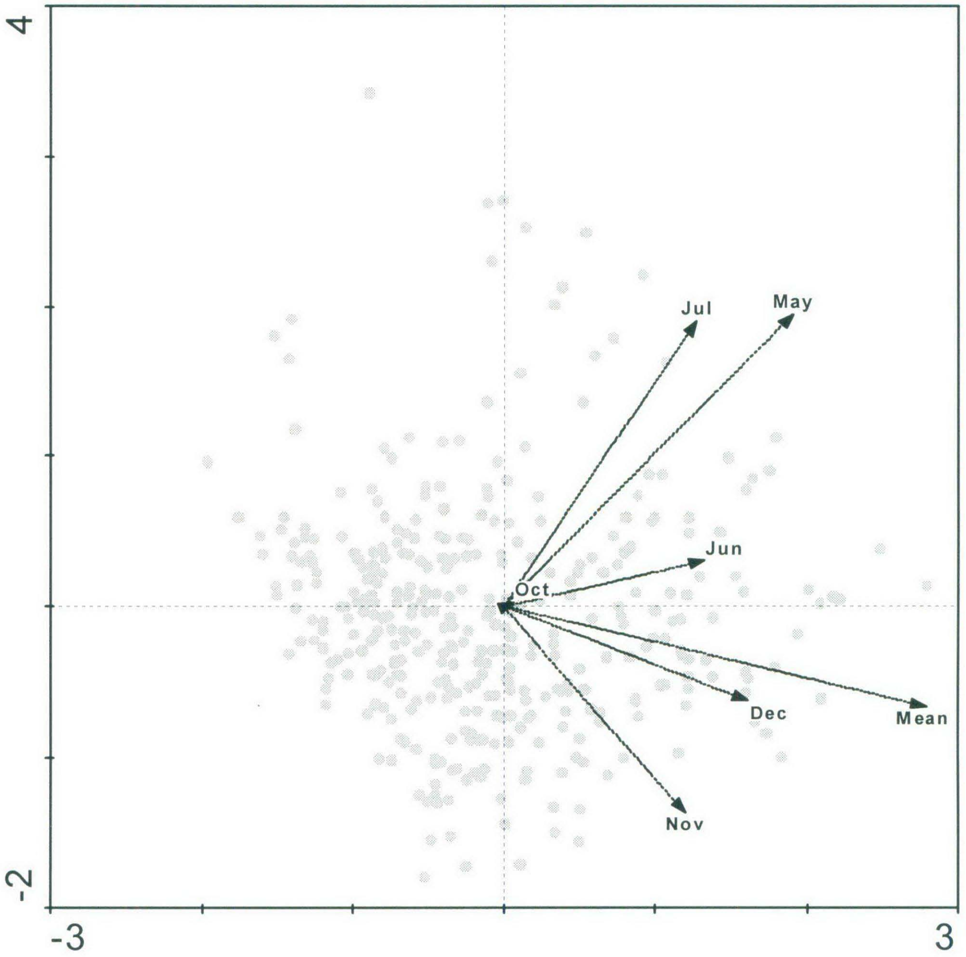

Figure 7.8 Site and radiation variable ordination biplot for CCA illustrating only significant variables. Sites, ●; radiation variables represented by vectors. Mean refers to the mean annual radiation.

Table 7.8 Species with the largest positive and negative associations with the increasing mean radiation vector in the species ordination biplot (Figure 7.8). Species frequencies calculated from n = 373 sites. Sorted by descending frequency.

Positive relationship with increasing mean radiation	Frequency (%)	Negative relationship with increasing mean radiation	Frequency (%)
Dianella revoluta var. *revoluta*	3	**Eleusine tristachya*	24
Gonocarpus tetragynus	3	*Cynodon dactylon*	23
Eucalyptus viminalis	3	**Phalaris aquatica*	20
Dianella longifolia var. *longifolia*	3	**Lolium perenne*	15
Hibbertia obtusifolia	3	**Festuca pratensis*	8
Pultenaea microphylla	2	**Dactylis glomerata*	8
Veronica calycina	2	**Modiola caroliniana*	6
Poranthera microphylla	2	**Arctotheca calendula*	3
Lomandra multiflora subsp. *multiflora*	2	**Bromus brevis*	3
Pimelea linifolia	2	**Gamochaeta spicata*	2

* Exotic species

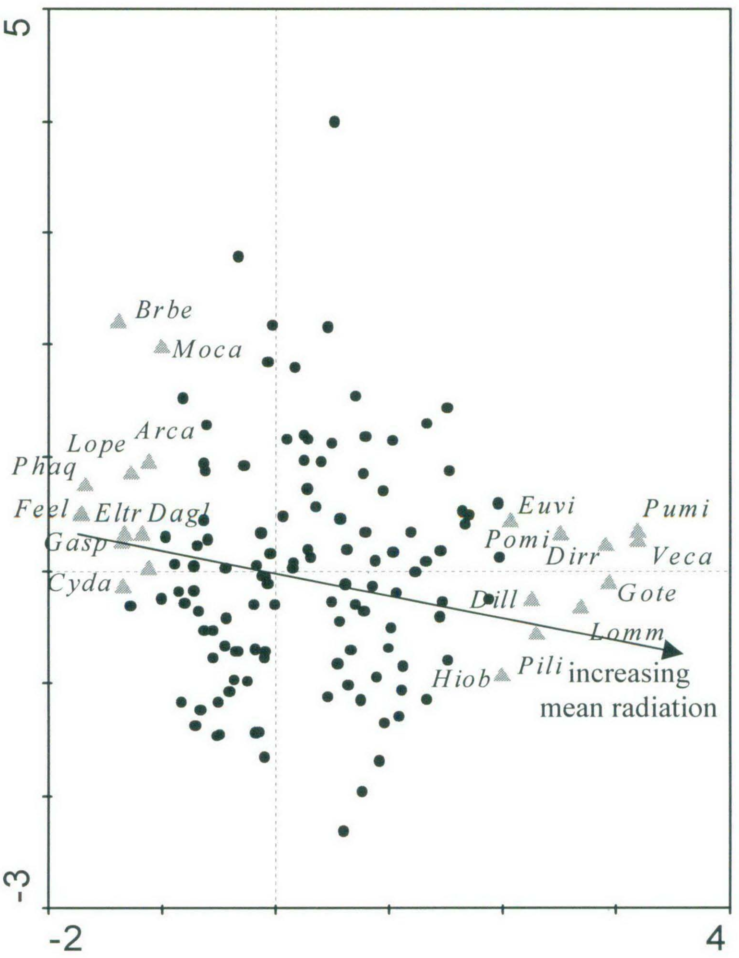

Figure 7.9 Species ordination biplot from CCA illustrating the ten species with the largest positive and negative associations with the increasing mean radiation vector. Unidentified species, •; identified species, ▲; temperature variable represented by vector. Species codes: *Arca – Arctotheca calendula, Bbre – Bromus brevis, Cyda – Cynodon dactylon, Dagl – Dactylis glomerata, Dill – Dianella longifolia* var. *longifolia, Dirr – Dianella revoluta* var. *revoluta, Eltr – Eleusine tristachya, Euvi – Eucalyptus viminalis, Feel – Festuca pratensis, Gasp – Gamochaeta spicata, Gote – Gonocarpus tetragynus, Hiob – Hibbertia obtusifolia, Lomm – Lomandra multiflora* subsp. *multiflora, Lope – Lolium perenne, Moca – Modiola caroliniana, Phaq – Phalaris aquatica, Pili – Pimelea linifolia, Pomi – Poranthera microphylla, Pumi – Pultenaea microphylla, Veca – Veronica calycina.*

Precipitation

Precipitation variables accounted for 9% of the explained variance. Precipitation variables that were not significant in the first forward selection analysis and were removed included August and November. Neither summer nor winter rain were significant, nor were October and July precipitation. Significant precipitation variables included those for the summer months, December to April, and winter months, May, June, and September. Mean annual precipitation was also significant (Table 7.9). Most of the significant precipitation variables were correlated and their vectors aligned in the upper left of the ordination plot, whereas the vectors for May and September were located in the lower left sector (Figure 7.10). The precipitation vector was orientated in the same line as the radiation vector but was opposite in direction. Species including *Pultenaea microphylla, Veronica calycina* and *Dianella revoluta* var. *revoluta* associated with high solar radiation, were located in sites with low precipitation. All species associated with high precipitation were exotic (Figure 7.11, Table 7.10).

Table 7.9 All forward selection results for precipitation variables in the CCA. Non- significant (p > 0.05) variables removed in the reduction of the data set after the first forward selection analysis are indicated by ^{z}. Sorted by ascending values of p.

Precipitation variable	F	p
Mean precipitation	2.22	0.002
January precipitation	1.87	0.002
March precipitation	1.87	0.002
February precipitation	1.72	0.002
December precipitation	1.56	0.002
June precipitation	1.49	0.002
April precipitation	1.40	0.002
May precipitation	1.33	0.002
September precipitation	1.23	0.020
October precipitation	1.14	0.108
August precipitation	1.05	0.290^z
July precipitation	0.99	0.504
November precipitation	0.98	0.528^z
Winter precipitation	0.06	1.000
Summer precipitation	0.02	1.000

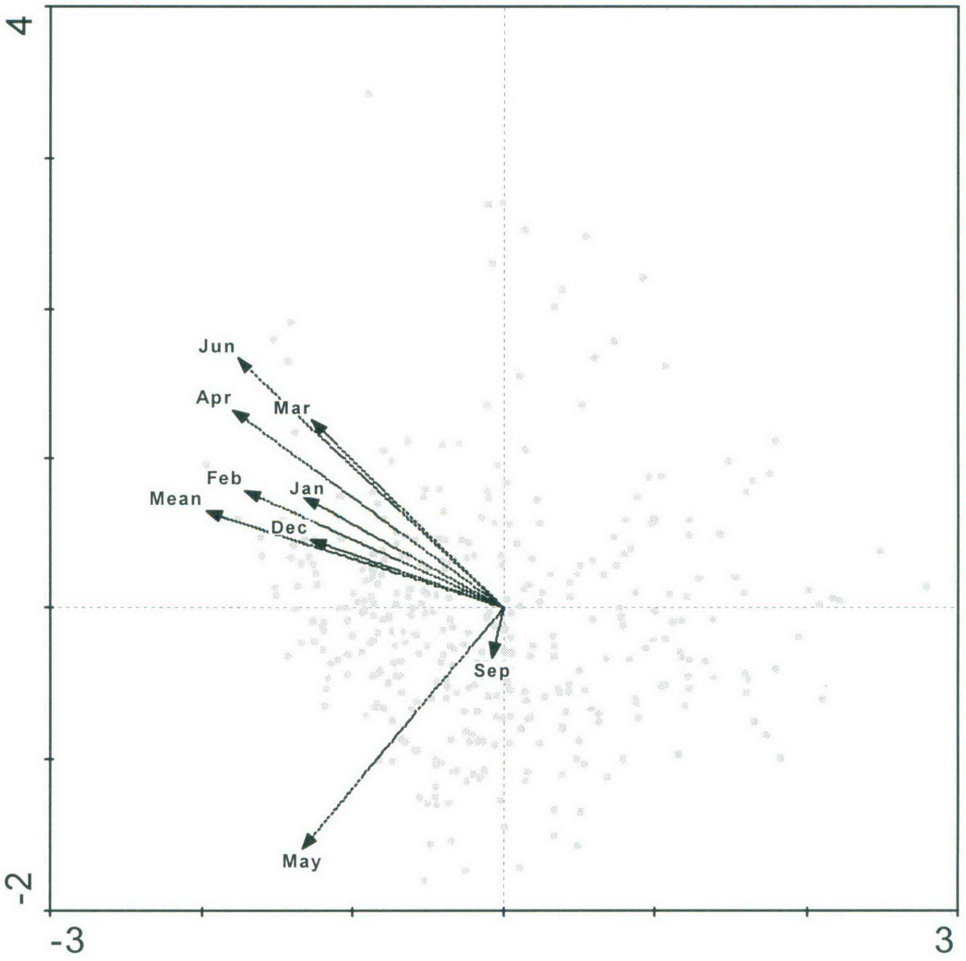

Figure 7.10 Site and precipitation variable ordination biplot for CCA illustrating only significant variables. Sites, ●; precipitation variables represented by vectors. Mean refers to the mean annual precipitation.

Table 7.10 Species with the largest positive and negative associations with the increasing June precipitation vector in the species ordination biplot (Figure 7.10). Species frequencies calculated from n = 373 sites. Sorted by descending frequency.

Positive relationship with increasing June precipitation	Frequency (%)	Negative relationship with increasing June precipitation	Frequency (%)
**Phalaris aquatica*	20	*Dianella revoluta* var. *revoluta*	3
**Lolium perenne*	15	*Dianella longifolia* var. *longifolia*	3
**Festuca pratensis*	8	*Gonocarpus tetragynus*	3
**Medicago laciniata*	6	*Hibbertia obtusifolia*	3
**Modiola caroliniana*	6	*Aristida calycina* var. *calycina*	2
**Polygonum aviculare*	5	*Aristida jerichoensis* var. *subspinulifera*	2
**Arctotheca calendula*	3	*Lomandra multiflora* subsp. *multiflora*	2
**Bromus brevis*	3	*Pimelea linifolia*	2
**Bromus cartharticus*	3	*Pultenaea microphylla*	2
Einadia nutans subsp. *nutans*	3	*Veronica calycina*	2

* Exotic species

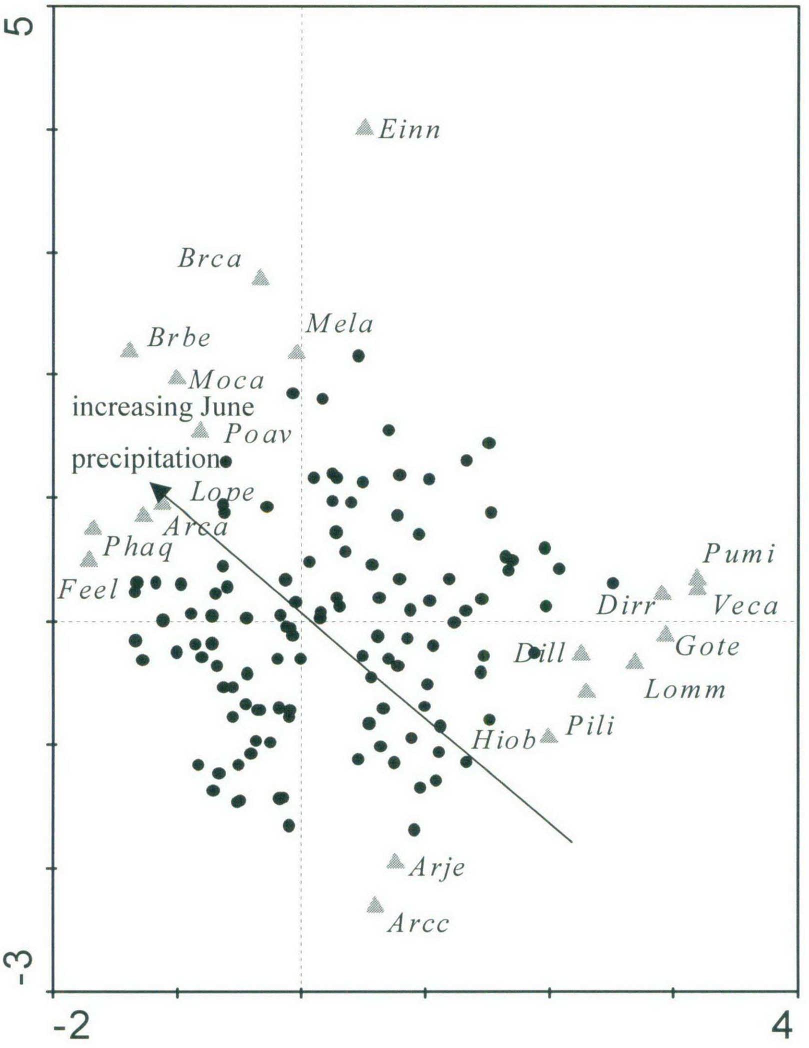

Figure 7.11 Species ordination biplot from CCA illustrating the ten species with the largest positive and negative associations with the vector of increasing June precipitation. Unidentified species, •; identified species, ▲; June precipitation variable represented by vector. Species codes: ***Arca - Arctotheca calendula, Arcc - Aristida calycina*** **var.** ***calycina, Arje - Aristida jerichoensis*** **var.** ***subspinulifera, Bbre - Bromus brevis, Brca - Bromus cartharticus, Dill - Dianella longifolia*** **var.** ***longifolia, Dirr - Dianella revoluta*** **var.** ***revoluta, Einn – Einadia nutans*** **subsp.** ***nutans, Feel - Festuca pratensis, Gote - Gonocarpus tetragynus, Hiob - Hibbertia obtusifolia, Lomm - Lomandra multiflora*** **subsp.** ***multiflora, Lope - Lolium perenne, Mela - Medicago laciniata, Moca - Modiola caroliniana, Phaq - Phalaris aquatica, Pili - Pimelea linifolia, Poav - Polygonum aviculare, Pumi - Pultenaea microphylla, Veca - Veronica calycina.***

Moisture Index

Moisture index accounted for 9.0% of the explained variance. Significant moisture index ratios included the months of May to October inclusive, December and January (Table 7.11). The ordination plot shows all the significant moisture variables in the upper left sector (Figure 7.12), and generally mirrors the ordination biplot for precipitation. Species associated with high moisture indices include seven species also associated with high precipitation, as well as *Einadia nutans* subsp. *nutans, Austrodanthonia bipartita* and *Chenopodium pumilio*. The three species associated with low moisture indices but not low precipitation were *Aristida vagans, Cheilanthes sieberi* subsp. *sieberi* and *Cymbopogon refractus* (Figure 7.13, Table 7.12).

Table 7.11 All forward selection results of moisture index ratio variables in the CCA. Non-significant ($p > 0.05$) variables removed in the reduction of the data set after the first forward selection analysis are indicated by ^{z}. Sorted by ascending values of p.

Moisture index ratio	F	p
June moisture index ratio	3.61	0.002
October moisture index ratio	2.06	0.002
July moisture index ratio	1.86	0.002
February moisture index ratio	1.54	0.002
September moisture index ratio	1.51	0.002
December moisture index ratio	1.49	0.002
August moisture index ratio	1.41	0.002
May moisture index ratio	1.40	0.002
April moisture index ratio	1.06	0.296^z
January moisture index ratio	1.04	0.342^z
November moisture index ratio	0.87	0.862^z
March moisture index ratio	0.37	1.000^z
Winter moisture index ratio	0.24	1.000

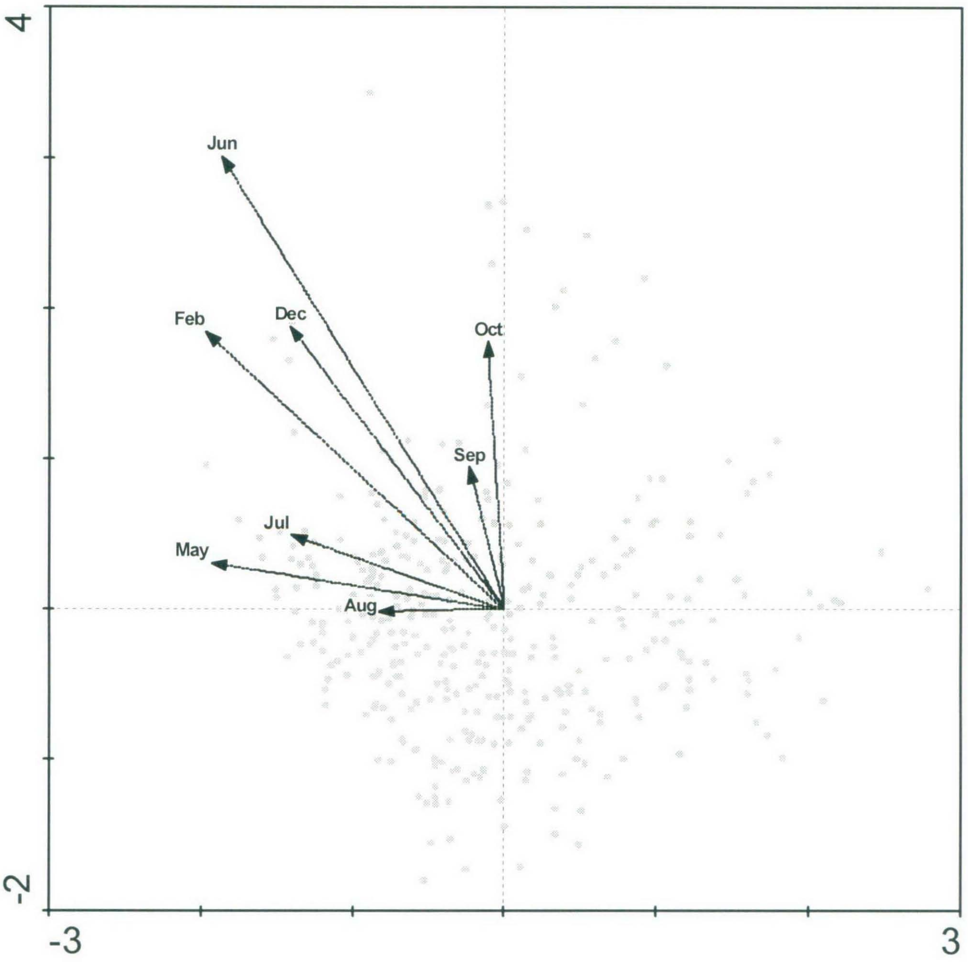

Figure 7.12 Site and moisture index variable ordination biplot for CCA illustrating only the significant variables. Sites represented by ●, and moisture index variables represented by vectors.

Table 7.12 Species with the largest positive and negative associations with the increasing June moisture index vector in the species ordination biplot (Figure 7.12). Species frequencies calculated from n = 373 sites. Sorted by descending frequency.

Positive relationship with increasing June moisture index	Frequency (%)	Negative relationship with increasing June moisture index	Frequency (%)
**Phalaris aquatica*	20	*Cheilanthes sieberi* subsp. *sieberi*	9
**Lolium perenne*	15	*Aristida vagans*	4
Austrodanthonia bipartita	7	*Cymbopogon refractus*	4
**Medicago laciniata*	6	*Gonocarpus tetragynus*	3
**Modiola caroliniana*	6	*Hibbertia obtusifolia*	3
**Polygonum aviculare*	5	*Aristida calycina* var. *calycina*	2
Einadia nutans subsp. *nutans*	3	*Aristida jerichoensis* var.	2
**Bromus cartharticus*	3	*Lomandra multiflora* subsp. *multiflora*	2
**Bromus brevis*	3	*Pimelea linifolia*	2

* Exotic species

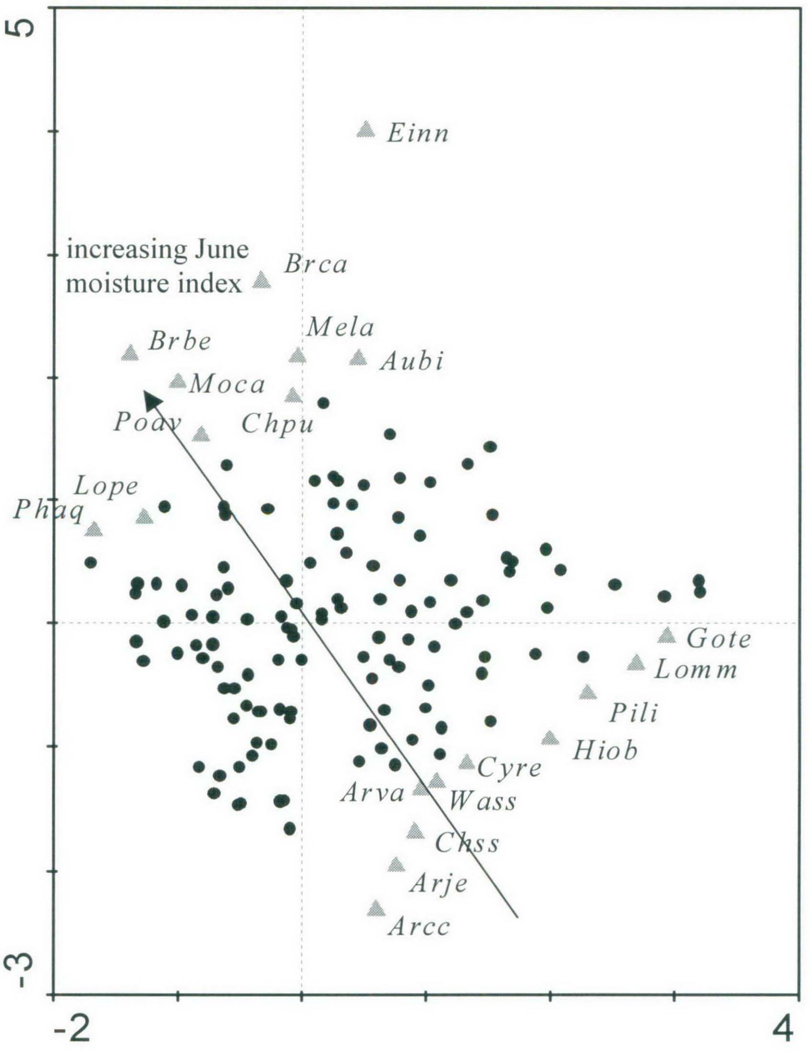

Figure 7.13 Species ordination biplot from CCA illustrating the ten species with the largest positive and negative associations with the increasing June moisture index. Unidentified species, •; identified species, ▲; June moisture index represented by vector. Species codes: ***Arcc – Aristida calycina*** **var.** ***calycina, Arje – Aristida jerichoensis*** **var.** ***subspinulifera, Arva – Aristida vagans, Aubi – Austrodanthonia bipartita, Bbre – Bromus brevis, Brca – Bromus cartharticus, Chpu – Chenopodium pumilio, Chss – Cheilanthes sieberi*** **subsp.** ***sieberi, Cyre – Cymbopogon refractus, Einn – Einadia nutans*** **subsp.** ***nutans, Gote – Gonocarpus tetragynus, Hiob – Hibbertia obtusifolia, Lomm – Lomandra multiflora*** **subsp.** ***multiflora, Lope – Lolium perenne, Mela – Medicago laciniata, Moca – Modiola caroliniana, Phaq – Phalaris aquatica, Pili – Pimelea linifolia, Poav – Polygonum aviculare, Wass – Wahlenbergia stricta*** **subsp.** ***stricta.***

7.3.4 Overall summary

The results from the CCA are summarised in Figure 7.14. Sites associated with commercial grazing (production) were generally to the left of the ordination plot, and management variables associated with grazing, cultivation and fertiliser application all projected into the lower left quadrant. Sites associated with land used for production occurred across the full range of lithology and soil nutrients.

Public sites were clustered in the lower right of the ordination plot, with these sites being characterised by high mean radiation indices. Trees were associated with private remnants in the upper right quadrant. Associated with public and private remnant land tenure were sites that were ungrazed or only episodically grazed. Other environmental variables (precipitation, moisture index, radiation and temperature) are summarised by one vector per variable cluster in Figure 7.14. At least one variable from each group was found to be associated with species composition.

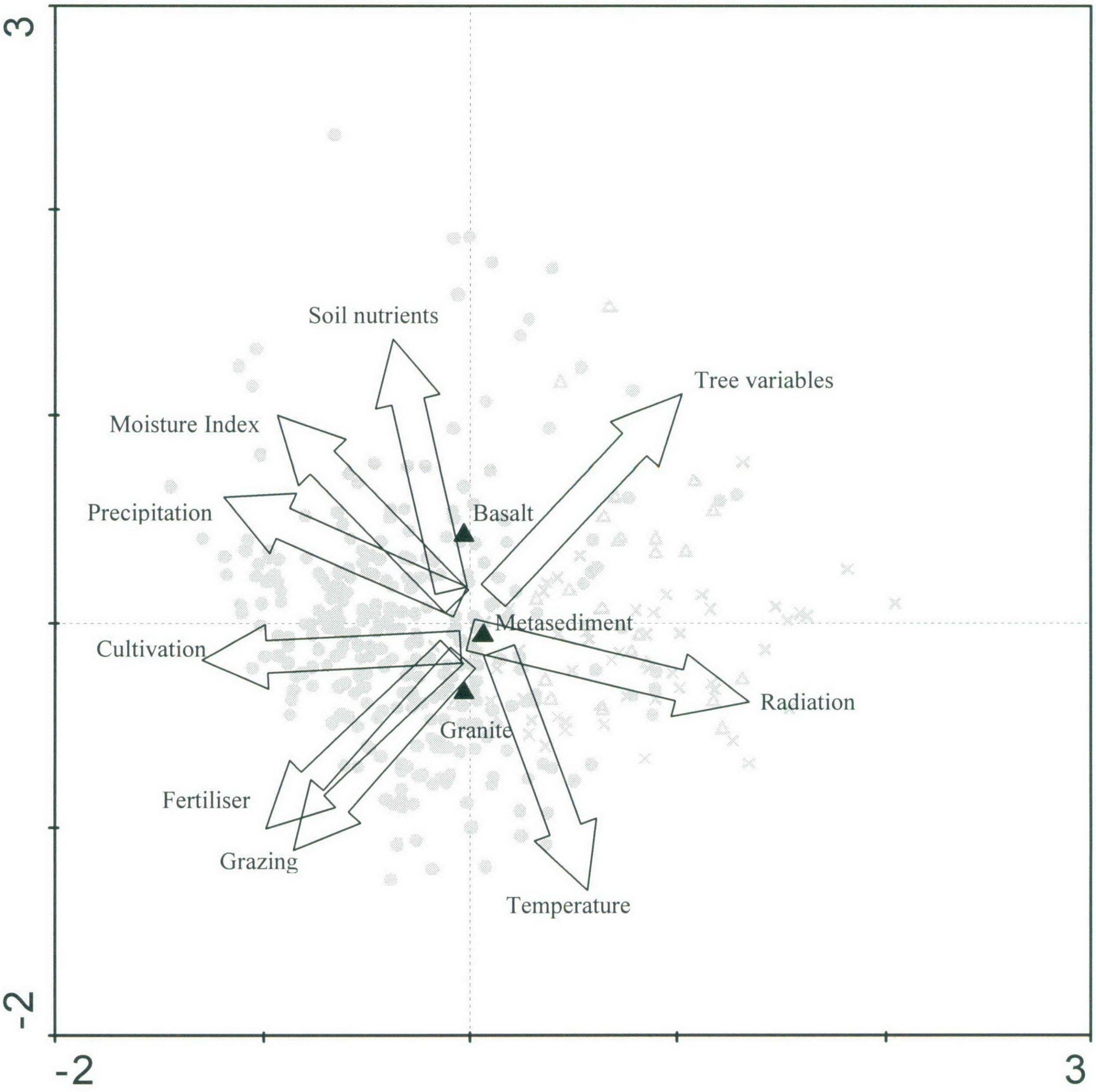

Figure 7.14 Schematic summary of the management and environmental variables influencing species composition on the Northern Tablelands of NSW. Not all variables represented. Land tenures: public, ×; production, ●; private remnant, △.

7.4 DISCUSSION

A large number of environmental variables were found to be significantly associated with the floristic composition of the ground-storey vegetation on the Northern Tablelands. The following discussion is ordered from the most to the least influential of the environmental variables based on the percentages of explained variation, with the exception of radiation which is discussed with other climatic variables.

7.4.1 Climate variables

Precipitation

Climatic variables were found to be associated with species composition. All species associated with increasing June precipitation were exotic C_3 grasses and herbs, and were generally associated or correlated with sites that had higher grazing pressure, a history of pasture development and fertiliser inputs (Section 4.3.3), leading to an overall increase in productivity per unit area. Production responses to precipitation have been studied extensively in Australia (e.g. Harris and Lazenby 1974; Walker *et al.* 1996) and overseas (e.g. Peacock 1976; Buckland *et al.* 2001; O'Connor *et al.* 2001; Jobbagy *et al.* 2002). These studies show that variation in biomass production is directly related to precipitation, although this response is most marked in semi-arid and arid systems but not confined to them. On the Northern Tablelands, higher rainfall is associated with increased pasture production (Nadolny, C., Whalley, R.D.B. and McIntyre, S. pers. comm. 4th July 2003). Rainfall is confounded with other environmental factors, most notably altitude (Figures 7.3 and 7.10) (McIntyre and Lavorel 1994).

Temperature

Extreme temperature ranges are generally relevant to plant adaptation, distribution and survival, as both heatwaves and frosts influence seasonal growth and species composition (Fitzpatrick and Nix 1975). Average temperatures on the Northern Tablelands generally do not exceed 30°C during the summer, and so heatwaves do not strongly influence species composition in the region (Lodge and Whalley 1989). Frosts can occur throughout the region mainly from April to September (Lodge and Whalley 1989; Burr 2003). On the Northern Tablelands, warm-season perennials grow throughout the summer and become dormant in autumn when lower temperatures, frosts and a lack of rainfall limit growth (Whalley and Bellotti 1997). Cool-season perennials commence growth in autumn and are frost tolerant and may make some growth in winter. Yearlong green perennial species provide forage throughout the year depending on conditions. The results of the present study show associations between minimum temperatures and the species composition of the regional ground-storey vegetation.

Species associated with the warmest temperatures in the study region included *Aristida calycina* var. *calycina, A. jerichoensis* var. *subspinulifera* and *A. vagans.* In general, *Aristida* species are moderately frost tolerant as well as drought tolerant (Kahn *et al.* 2003). Other species associated with higher temperatures included *Cymbopogon refractus* and *Setaria* species and these also have low frost tolerance (Kahn *et al.* 2003). Their presence at sites associated with high temperatures may be due to sensitivity to frosts and cold temperatures, but is more likely to be due to their presence in warmer, drier environments with no fertiliser and cultivation because of lesser returns (Section 4.3.4) in such areas. *Austrodanthonia bipartita, Medicago laciniata* and *Bromus* species were associated with low temperatures and are all frost tolerant (Kahn *et al.* 2003). These species are evidently able to withstand extremes of low temperature.

Moisture index

Moisture index was the most influential climate variable after temperature and precipitation, based on the percentages of explained variation. It was calculated as the ratio of precipitation to evaporation (Section 4.2.4). The explanation of the influence of moisture index is closely aligned with that of precipitation. Soil moisture is the variable most limiting to primary production over most of Australia (Fitzpatrick and Nix 1975), either due to the small amount of rainfall or the seasonal nature of rainfall in wetter regions. The Northern Tablelands climate is cool temperate with the majority of rain falling in the summer months (Lodge and Whalley 1989). Generally the winters are dry and cold, with frequent frosts, but the moisture index is more reliable in winter due to less evaporation. Moisture index is important in deciding when to plant sown pastures dominated by *Trifolium* and *Medicago* species, as the sowing of these pasture species generally requires a constant moisture index with relatively little deficit (Fitzpatrick and Nix 1975; Scott 1997) . The Northern Tablelands has a relatively high moisture index during winter, summer and over the driest period of the year (April - August), making it an ideal climate for sowing introduced pasture species (Fitzpatrick and Nix 1975). This has led to the dominance of exotic species in many pastures in the region. A high moisture index was associated with mainly introduced C_3 pasture species including *Phalaris aquatica, Lolium perenne, Medicago* species and *Bromus* species. However, high moisture indices were significantly correlated with altitude (Section 4.3.4) and also was strongly associated (but not significantly) with the sowing of New England pasture mix and associated fertiliser regimes. The responses observed for the native species such as *Aristida* species, *Cymbopogon refractus* and *Cheilanthes sieberi* (Kahn *et al.* 2003) most likely reflect a close association with a lack of pasture development (i.e. areas that were not cultivated, fertilised or grazed).

Radiation

Solar radiation is a crude index of the light environment but is useful in discussing the light requirements of plants (Fitzpatrick and Nix 1975). Generally, values of solar radiation are high in summer, although this can vary in very high rainfall locations. The species associated with high solar radiation were all native, but did not include any grasses. The mean annual solar radiation was correlated (although not significantly) with axis 1 which was characterised by variables associated with private remnant and public land, which has not undergone any agricultural intensification (i.e. not grazed, fertilised or cultivated). Shrubs such as *Hibbertia obtusifolia* and *Pultenaea microphylla* and lilies such as *Dianella* species persist in these areas, in the absence of grazing, fertiliser and cultivation. In contrast, species associated with relatively low radiation were predominantly exotic pasture grasses (mostly C_3) including *Phalaris aquatica, Lolium perenne, Festuca pratensis* and *Dactylis glomerata*, reflecting sites that have undergone intensive agricultural development through fertiliser application, cultivation and associated increases in stocking rate, grow predominantly in late winter and spring and are generally dormant over summer (FitzGerald and Lodge 1997).

Climate variables may be important in explaining ground-storey relationships in other studies in the region (e.g. McIntyre *et al.* 1993; Benson and Ashby 2000; Waters 2001; Clarke 2003). Clarke (2003) concluded ground-storey composition was most strongly related to disturbance, where as McIntyre and Lavorel (1994) ranked disturbance and environmental factors equally. Consideration of climatic variables in these studies may have explained greater percentages of the variance, or resulted in different conclusions as to the relative importance of disturbance and environmental factors explaining vegetation composition.

7.4.2 Soil nutrients

Soil nutrients (pH 1:5 $CaCl_2$, sulphur, phosphorous, organic carbon and nitrogen) were positively correlated with variables associated with increasing agricultural intensity including high levels of fertiliser application and basalt lithology in production land use/tenures.

Species associated with increasing phosphorus and nitrogen nutrient levels includes a number of exotic species including *Bromus catharticus* and *B. brevis*. Both species occur in greater numbers on fertile soils (Kahn *et al.* 2003). *Medicago laciniata* and *Taraxacum officinale* are also more abundant on fertile soils (Kahn *et al.* 2003). Of the five native species strongly associated with elevated soil nutrients, *Austrodanthonia bipartita* is one of many congeners in the region known to increase in response to fertility (Lodge and Whalley 1989). Hester and Hobbs (1992) found that the abundance of non-native species in shrubland in Western Australia was related to soil phosphorus levels. A similar result was found in the present study.

The species associated with lowest soil fertility were predominantly native, and may be sensitive to increasing soil nutrients and associated agricultural activities. *Aristida* species decrease in response to fertility (Lodge and Whalley 1989) and therefore it is not unexpected that *Aristida vagans, A. calycina* var. *calycina* and *A. jerichoensis* var. *subspinulifera* were all associated with low fertility. *Cymbopogon refractus* was closely located with the *Aristida* species in the ordination plot, and is known to decline with fertility and the associated increase in grazing pressure (Lodge and Whalley 1989). Herbs including *Wahlenbergia stricta* subsp. *stricta, Cheilanthes sieberi* subsp. *sieberi* and *Solenogyne bellioides* associated with low fertility may be sensitive to increasing fertility or the associated increase in competition. Kahn *et al.* (2003) stated that *Cheilanthes* does not respond to improved soil fertility but little is known about its sensitivity to nutrient enrichment.

Soil chemistry was correlated with changes in species composition of the ground-storey vegetation on the Northern Tablelands. This result concurs with the conclusions of Prober *et al.* (2002a), who found that species composition varied with soil properties on the Southern Tablelands of NSW. They showed that species composition changed in response to a gradient in soil productivity.

7.4.3 Other variables

Lithology

Lithology significantly influenced species composition in the present study, consistent with previous research on the Northern Tablelands of NSW (see Benson and Ashby 2000; Clarke 2003), and elsewhere (e.g. Bean and Whalley 2001; Prober *et al.* 2002b). Basalt parent material on the Northern Tablelands is inherently more fertile than granite or metasediment. Granite is the least fertile of the three lithologies sampled. Species associated with the basalt centroid were predominantly native and exotic annuals such as *Conyza albida* and *Plantago lanceolata. P. lanceolata* is recorded as increasing with improved fertility (Kahn *et al.* 2003). Metasediment and granite parent materials were characterised by the exotic annual, *Hypochaeris glabra/radicata,* which is common in grazed pastures (Kahn *et al.* 2003), and the native herb, *Euchiton sphaericum.*

Geographical position

Geographical position (East – West) was positively associated with a change in species composition on the Northern Tablelands, as concluded by Waters (2001). Easterly areas near the Apsley-Macleay River gorge lands and escarpment of the Great Dividing Range have a higher annual rainfall (up to 2000 mm in some areas) (Morgan and Terry 1999) compared to Armidale in the centre of the study region (790 mm p.a.; Commonwealth Bureau of Meteorology 2002). Locations further west receive less annual rainfall. Combined with rainfall are the effects of location on species composition with changing proximity to adjacent botanical divisions. Floristic changes in the east occur as one approaches the coastal division, which is largely subtropical, as well as in the west where one approaches the North West Slopes which is drier and warmer than the Tablelands and is more influenced by westerly rain bearing systems in winter and less influenced by summer moisture bearing easterly systems (Harden 1993a). Exotic species encroaching from the east include *Paspalum urvillei* and *Sporobolus elongatus*, while *Hyparrhenia hirta, Nassella neesiana, Eragrostis curvula* and *Panicum maximum* make inroads from the north, northwest and west (Whalley, R.D.B. pers. comm. 5th September 2003). Only *Eragrostis curvula* and *Panicum maximum* were recorded in this survey. Species positively associated with geographical position East – West were predominantly exotic, while native species were associated with the most westerly locations. These results are correlated with the influences of altitude, precipitation and moisture indices (Section 4.3.4)

Site variables

Altitude and slope were found to be associated with changes in species composition. Altitude must be considered carefully as the effect of altitude is often confounded with lithology: basalt sites generally occur at higher elevations and metasediment lithologies at lower altitudes on the Northern Tablelands (McIntyre and Lavorel 1994), as in this study. Sites at higher elevation in the east and north of the study region experience increased rainfall (McIntyre and Lavorel 1994, Table 2.1).

Altitude was positively correlated with variables related to intensification of agriculture, particularly fertiliser variables (Section 4.3.4) These factors are likely to result in increased stocking pressure on sites that are more likely to have sown pasture grasses due to agricultural intensification including the species *Lolium perenne, Phalaris aquatica, Dactylis glomerata,* and associated *Trifolium* and *Medicago* species. Lower altitudes were associated with the pin rush, *Juncus usitatus*, which has a preference for duplex soil profiles in which drainage is impeded on granite and metasediment lithologies which are more frequent at lower altitude. *Aristida vagans, A. calycina* var. *calycina* and *A. jerichoensis* var. *subspinulifera* occur in soils of low fertility (Lodge and Whalley 1989), particularly granites, which are more common at lower altitudes.

Slope was correlated with species composition in this study, as has been found in other Australian studies (King 2002) and elsewhere (Hester *et al.* 1999). Hester *et al.* (1999) concluded that slope affects patterns of herbivore use and impact, as animals have a reluctance to face downhill when grazing. The effect of slope often cannot be differentiated from that of aspect, position in the landscape or landscape element, so various studies have examined microclimate rather than these individual factors. Herbs, *Poranthera microphylla* and *Veronica calycina*, were associated with increasing slope. Their preference for increasing slope may be related to the patterns of herbivore use on slopes (Hester *et al.* 1999), and to areas having not been cleared for agricultural production and therefore remaining dominated by native species. Flat and low slope sites were associated with the grasses, *Festuca pratensis, Eragrostis benthamii, E. benthamii, E. molybdea, Cynodon dactylon* and *Lachnagrostis aemula*, which are species that increase in response to grazing (Lodge and Whalley 1989), most likely reflecting herbivore grazing patterns and agricultural intensification on flatter land.

Aspect was not correlated with species composition, which contrasts with the findings of Bean and Whalley (2001) and Hutchings (1983). This study was different from Bean and Whalley (2001) and Hutchings (1983), as aspect was not constrained. In their studies, Bean and Whalley (2001) limited site selection to two opposing aspects on the Liverpool Plains, NSW, and Hutchings (1983) to four contrasting aspects in south-eastern England. Previous studies (McIntyre *et al.* 1993; Clarke 2003) have not deduced that aspect is important in determining species richness or species composition. If aspect does influence ground-storey vegetation on the Northern Tablelands, it is likely that it does so through microclimatic effects on species in combination with other physical variables that may be better summarised by radiation or moisture indices.

Although position in the landscape – accumulating water was not associated with species composition in this study, position in the landscape is important for many reasons, including surface and subsoil water movement and soil temperature. These factors create a microhabitat, where moist areas or areas accumulating water are more likely to accommodate species that prefer such conditions, such as *Juncus usitatus, J. filicaulis, J. vaginatus* and *Pennisetum alopecuroides*. *P. alopecuroides* and *Juncus* species occur in the region on granite soils where water comes close to the surface as a result of subsurface lateral flow (pers. obs.). McIntyre and Lavorel (1994) found that species composition was affected by water accumulation from increased runoff due to human influences such as the construction of roads. Although water enrichment in this study was not due to earthworks as it was in the study of McIntyre and Lavorel (1994), a similar result can be expected. It is likely that other variables such as slope subsumed the explanatory significance of position in the landscape in this study.

Tree cover

Tree cover accounted for 2% of the explained variance. Other studies on the Northern Tablelands (Reid *et al.* 1997; Gibbs *et al.* 1999; Clarke 2003) have found that trees are an important determinant of the vascular plant species under the canopy. Sites influenced by trees were deliberately not sampled in paddocks that had a history of cultivation or fertiliser application by ground methods rather than aerial application, as the effect of cultivation and fertiliser could not be reliably established. Stock camps were also avoided. As a consequence, the percentage of sites influenced by tree canopies was low (25%). Despite the low number of sites affected by trees, several species were associated with them. Sites associated with trees were often located in private remnant patches or roadsides (uncleared areas) and therefore the results are correlated with the absence of grazing, cultivation and fertiliser application (Section 4.3.4). Subshrubs and shrubs such as *Einadia nutans* subsp. *nutans, Gonocarpus tetragynus* and *Pultenaea microphylla* were associated with tree cover. These species are thought to be either sensitive to grazing or cleared from the original landscape or both (Clarke, P. J. pers. comm. 4th June 2003), as reflected in their position in the opposite sector from grazing and associated management variables in the ordination diagram.

Other studies have found that trees reduce pasture production, or occasionally increase production, as trees compete with or facilitate growth of ground-storey vegetation (McIntyre 2002). Various hypotheses exist to explain why species assemblages vary beneath trees and these include reduced yields, increased soil fertility and microclimate modification (Burrows *et al.* 1988; Gibbs *et al.* 1999).

7.4.4 Conclusions

This study has demonstrated that environmental variables are likely to have important and perhaps overlooked influences on species composition, although their influence in frequently correlated with management variables such as agricultural intensification. These results have important ramifications for the design of similar studies as climate variables should be included in the stratification or as covariables in the interpretation and explanation of data. Fertility effects should be considered in future studies investigating ground-storey composition, as many native herbs including *Wahlenbergia stricta* subsp.

stricta, Cheilanthes sieberi subsp. *sieberi* and *Solenogyne bellioides* may be sensitive to increasing fertility. The influences of lithology, trees and geography on species composition corroborate earlier studies, and questions about the influence of slope and aspect require further investigation.