Association between environmental factors and the occurrence of six fumitory species (*Fumaria* spp. L.) in southern-eastern Australia

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Abstract

The occurrence of *Fumaria* as a weed in south-eastern Australian cropping systems is believed to have increased substantially in recent decades. To study this, a survey was conducted in contrasting regions of this zone, viz. southern New South Wales, mid-north South Australia. The survey analysed the pattern of occurrence of each of the six naturalized species found (*Fumaria bastardii*, *F. densiflora*, *F. muralis*, *F. officinalis*, *F. parviflora* and *F. capreolata*) and the natural environmental factors associated with their distribution. While five species were primarily found in agricultural environments, *F. capreolata* occurred exclusively in non-agricultural situations characterized by the presence of high soil organic matter. *F. densiflora* and *F. bastardii* were the most widespread and abundant species. *F. officinalis* was the rarest.

Environmental factors were significantly associated with the occurrence of each species. Soil texture and/or rainfall during one of the autumn months were important. Factors associated with some species overlapped with other species and it was common to find more than one species at a site. Occurrence over a wide range of soil types in some species suggests the presence of substantial bio- and ecotypical heterogeneity.

Keywords: Generalized linear model, multiple logistic regression, weed distribution.

Introduction

The members of the genus *Fumaria* L., known as fumitory or carrot weed in Australia, are annual herbs of semi-erect, trailing or climbing habit, ranging in origin from Western Europe, throughout the Mediterranean Basin and eastward to the Indian Subcontinent. About 50 different species are recognized world-wide, some of which occur as weeds in agricultural or horticultural crops (Sell 1964, Lidén 1986). However, Australian herbarium records and associated state and nation-wide Flora works suggest that only seven species are present: *Fumaria bastardii* Bor., *F. capreolata* L., *F. densiflora* DC., *F. muralis* Sonder ex Koch, *F. officinalis* L., *F. parviflora* Lam. and *F. indica* (Hauskn.) Pugsley (Toelken 1986, Harden 1990, Walsh 1994). While *F. indica* appears to be restricted to inland areas of Australia, all remaining species occur in the southern winter cropping zone.

In considering the abiotic factors that control the distribution of vegetation communities and plant species, the works of Woodward and Williams (1987) and Brown (1984) were important in emphasizing the influence of minimum temperature and moisture availability. Species that become weeds are a unique case however, because human management of the ecosystem or some other human interaction with the plant itself can be instrumental in facilitating the development of these species into weeds (Grime 1979). An historical overview of the weed surveys of the south-eastern Australian cropping zone suggests a substantial increase of *Fumaria* occurrence. In the 1960s, fumitory was found in less than 4% of crops in southern New South Wales (Taylor and Lill 1986), although occasional serious infestations were noted. By the early 1990s, the proportion of cereal crops infested with fumitory had risen to 36% in the same area (Lemerle *et al.* 1996). In Victoria, Wells and Lyons (1979) showed large regional variations in its occurrence with 8 to 36% of cereal crops infested. Velthuis and Amor (1982/83) observed that, despite being present in only 4% of south-western Victorian cereal crops, the average magnitude of its infestations meant that it ranged from the sixth to tenth most abundant of the 38 weeds recorded. In a survey of canola (*Brassica napus* L.) crops, Lemerle *et al.* (1999), found fumitory in 42% of the fields. Indeed, it is possible that the substantial increase in the area sown to canola across this zone in the last 20 years may be associated with the increasing incidence of fumitory. There are two factors that may be related to this increased fumitory incidence. Firstly, there are no herbicides capable of selectively removing fumitory from canola, and secondly, if fumitory seed is harvested together with canola, its similar size precludes the possibility of decontaminating the canola seedlot. This scenario indicates that canola seedlots might be a means whereby fumitory is spread further across the cropping zone and indeed fumitory has been found in canola seedlots (Norton 2003).

The work reported here is apparently the first attempt to survey exclusively the distribution of this genus anywhere in the world. Consequently there is little information available about the natural distribution of the genus. No previous surveys within Australia, which have included fumitories within the suite of weeds under study, have identified it beyond the genus and none has attempted to associate its occurrence with any environmental descriptors. Anecdotal information indicates there are differences in susceptibility of the different fumitory species to herbicides. Therefore, to begin to develop an understanding of the distribution of fumitory across the cropping zone it is essential for weed control purposes to identify plants to the species level. The research reported here is the first fumitory survey reporting at the species level in Australia.

To begin to address this shortfall, a targeted survey was carried out in two contrasting regions of the south-eastern cropping zone designed to: (i) identify natural environmental factors of soil, climate and topography associated with species occurrence, and (ii) extend understanding of the areas of distribution for each *Fumaria* species.

Materials and methods

Survey

The high potential for plants of the *Fumaria* genus to become serious crop weeds and the lack of knowledge of the environmental factors influencing its distribution provided the basis for the survey. As it was not feasible to survey the entire southern Australian cropping zone where fumitory has been known to occur, it was considered that an understanding of the environmental influences could be achieved by keeping latitude constant while varying rainfall distribution and soil type. The first region covered part of the South Australian wheat belt and experiences a typical Mediterranean type climate with distinctly dry summers and cool, moist winters. Soils are predominately neutral to alkaline, and 20% of the sites in the survey were in that region. The second region, comprising 80% of the survey sites, was characterized by intermittently storm-prone summers, cool-moist winters and acidic soils. This region extended from northern Victoria to the northern boundary of the winter cropping area in central New South Wales (Figure 1).

The survey was undertaken from early July to the end of September. To maximize the number of samples found, areas of known *Fumaria* presence were surveyed predominantly. From a randomly chosen starting point in the designated area, crops were inspected at intervals of approximately 10 km if *Fumaria* was present, or less, if absent. Regions with undulating topography were sampled at greater intensity. At each point, latitude, longitude and altitude were recorded with a Trimble Scoutmaster GPS™.

Where *Fumaria* was found, both plant and soil samples were collected whereas where it was not found, only soil samples were taken. Topographical details including aspect and position in the landscape, as well as the presence of limestone or rocks was recorded. In total 161 sites were surveyed, 146 of which were agricultural.

Where it was not possible to identify *Fumaria* seedlings, plants were collected to grow for later identification at flowering.

Soil variables

Soil texture was identified as either sand, sandy loam, loam, clay loam, light clay or medium-heavy clay (Northcote 1979). In addition, the following soil chemical parameters were determined: pH and electrical conductivity (EC)(1:5 soil:0.01 mol L^{-1} $CaCl_2$ extraction), K, Na, Ca, Mg, Al and Mn ($BaCl_2/NH_4Cl$ extraction) with subsequent calculation of Effective Cation Exchange Capacity (ECEC) as described by Rayment and Higginson (1992), total C, total N and total S (Dumas digestion; LECO analysis) and available (Olsen) P (micro-Kjeldahl digestion). The ratios and proportions: K %ECEC, Na %ECEC, Ca %ECEC, Mg %ECEC, Al %ECEC, Mn %ECEC were calculated as they are indicators for soil physical properties or plant nutritional problems (Edwards 1985, Shaw 1985, Smith 1985).

Climate variables

Climatic data were estimated using the MetAccess® database. Utilizing the GPS-coordinates, the nearest weather stations provided rainfall and/or temperature data for each survey point.

Average annual rainfall was used to describe the zones where *Fumaria* was found. Average monthly rainfall and temperature values between April 1 and June 30 were also collected as these months delineate the period of peak germination of all *Fumaria* species.

Statistical analysis

A range of different statistical procedures and models are available to analyse potential weed distributions (Kriticos and Randall 2001). In this survey a generalized linear modelling approach employing stepwise multiple logistic regression was a central component of the statistical analyses. This method is increasingly utilized and was preferred here because of its ability to relate the occurrence of a species (dependent variable) to multiple environmental parameters (independent variables) (Saab 1999, Collingham *et al.* 2000, Grundy and Mead 2000, Corbacho *et al.* 2003).

Due to the categorical nature of several survey variables, logistic regressions with binary response variables (0 = absent, 1 = present) were used and their significance was subsequently assessed by analysis of deviance (McCullagh and Nelder 1986). Logit transformations ensured that the modelled probabilities could only take values between 0 and 1.

The probability *P* of the occurrence of the response *y*, where influenced by an independent predictor variable *x* of sigmoidal shape (with a monotonic increase or decrease) and determined by the parameters b_0 and $b_{1,}$ was expressed by the equation:

$$P(y) = \frac{e^{(b_0 + b_1 x)}}{1 + e^{(b_0 + b_1 x)}}$$

Since *y* was a binary response variable that could only be 1 or 0, it was possible to calculate the odds of event 1 (presence) by dividing its probability by that of event 0 (absence) at a certain level of *x*. The change between the odds of event 1 at two different levels of *x* was described by the odds ratio *OR* (Neter *et al*. 996). These authors showed that, upon transformation, an OR of 2 between two odds of event 1 at points with a difference of 10 units of *x*, means that the odds of event 1 will double with each 10-unit increase of *x*. The cut-off point of *P* for the occurrence of event 1 was also determined to identify prediction errors. For this purpose, those values were obtained where the overall prediction error was minimized.

Pre-processing of data determined whether independent variables should be included in the multiple regressions to reduce dimensionality and collinearity. This was necessary because, in some species, the number of independent variables exceeded the number of data points and because high correlations between some x-variables would have led to an ill-conditioned model with unstable parameter estimates. Therefore, the following pragmatic, but widely used (e.g. Grundy and Mead 2000), three-step approach was applied using GenStat for Windows (5th edition, Release 4.2, Payne *et al*. 1994):

i. With each *Fumaria* species considered as the dependent variable and each of the environmental factors the independent variables, simple logistic regressions were undertaken. Initially, all regressions were calculated using the complete data set of 161 sites although subsequently data points from non-agricultural areas were excluded in the species that primarily occurred in agricultural areas, i.e. all species except *F. capreolata* and *F. muralis*, as these sites exerted unacceptable leverage in shaping the slope of the regression function. Indeed, as the main interest of the survey was the exploration of *Fumaria* presence in agricultural areas, the data from only the 146 agricultural sites were used for *F. bastardii*, *F. densiflora* and *F. parviflora*.
ii. Correlations between independent variables were assessed using simple linear or logistic regressions of each variable against each of the others to exclude correlated variables from the next step. Variables were considered correlated if the regression equation was significant and explained at least 70% of the variance.
iii. Stepwise multiple logistic regressions with all uncorrelated, significant independent variables obtained in step (1) were calculated in upward and downward progression, and significant variables were determined by analysis of deviance.

Results

Variation in occurrence of fumitory species and environmental factors

Most agricultural sites (AS) were in New South Wales (83%) while the majority of non-agricultural sites (NAS), where all *F. capreolata* samples were found, occurred in South Australia (67%) (Table 1). *F. densiflora* and *F. bastardii* were by far the most common species throughout the survey area, occurring at slightly more than 50% of all sites in New South Wales and 30 and 15%, respectively, of all sites in South Australia (Table 1). Both species were mostly found in AS but rarely in NAS (Figure 1, Table 1). In contrast, *F. capreolata* never occurred at AS whereas 25% of sites with *F. muralis* were NAS (Table 1). *F. parviflora* was relatively frequent in South Australia, but was rare in New South Wales, while *F. officinalis* was rare in both States (Table 1).

The mean annual rainfall of AS and NAS differed only slightly, although their ranges and monthly distributions varied substantially (Table 2). Among the AS, there was a difference of 40 to 50 mm between the minimum and maximum average monthly rainfall over autumn. Most NAS were in South Australia where several were located at the foot of the Mt. Lofty Ranges where more rainfall was received later in the season than elsewhere.

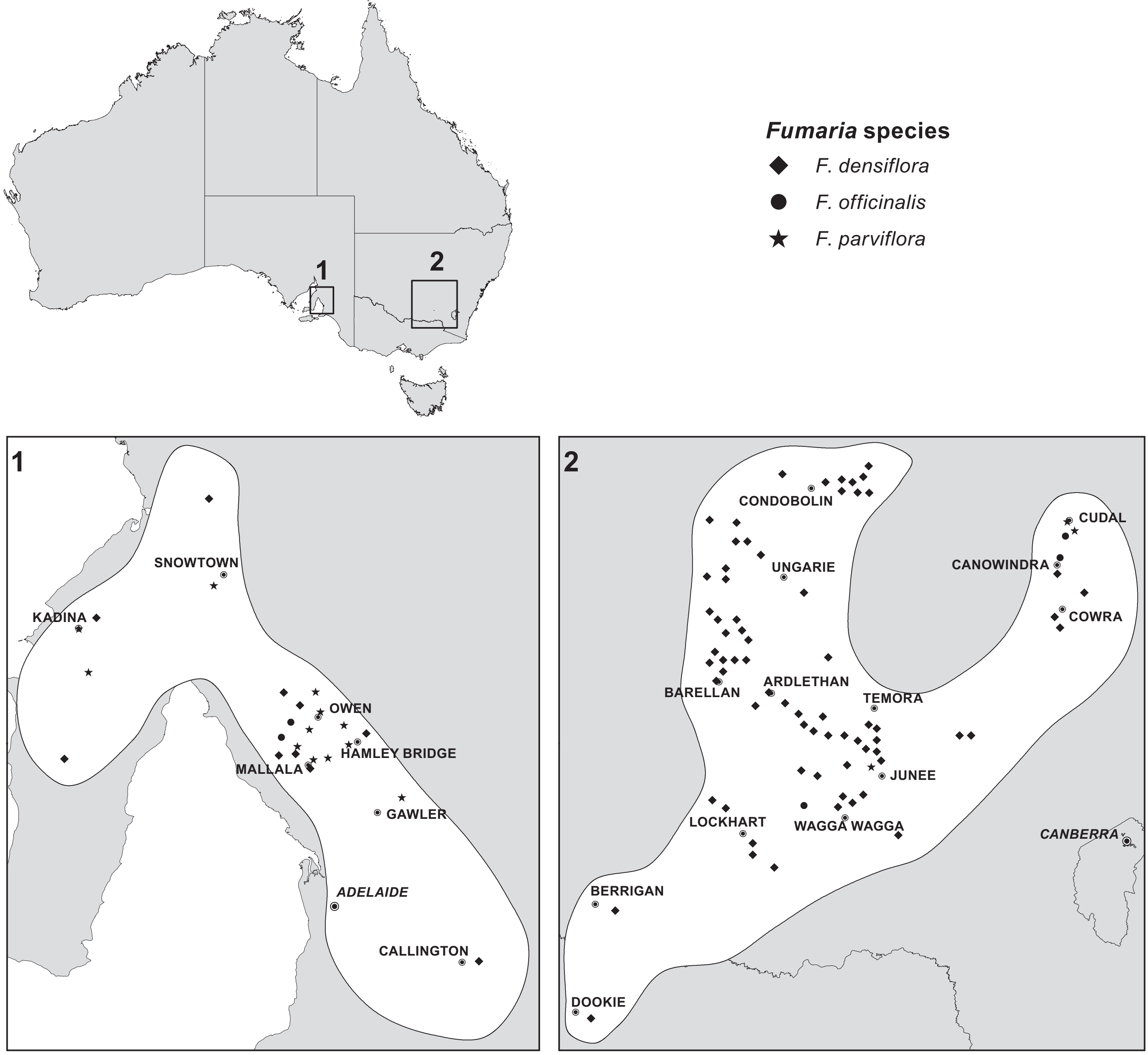

Figure 1 (a). Approximate areas of the survey together with the collection locations in southern New South Wales/ northern Victoria and South Australia of the narrow-leaved *Fumaria densiflora*, *F. officinalis* and *F. parviflora*.

Moreover, the range of annual rainfall was much higher in the NAS than the AS. However, there was no difference in temperatures between AS and NAS during the three autumn months when the temperature range was approximately 4°C (Table 2).

While about 50% of all AS were located on clay soils and approximately 10% on sands, 50% of the NAS had sandy soils and 20% were on heavier soils (Table 1). The differences in soil analyses between AS and NAS appeared to be related to the type of sites where *F. capreolata* was found, since these had higher amounts of leaf litter resulting in higher organic matter contents and elevated levels of total N, available P, ECEC and associated macro-nutrient cations. In addition, a larger proportion of the NAS had a higher average Na content due to proximity to the sea, high levels of calcium carbonate and the occurrence of limestone chips (a common feature in South Australian soils). This explains the higher Ca and pH of NAS soils and the substantially lower Al levels. The lower Mn levels found were associated with the more frequent occurrence of lighter, well-drained soils among the NAS (Table 2). No toxic levels were observed in any soils, although the value of 1 cmol kg^{-1} exchangeable Al can be yield-reducing in some crops (Edwards 1985). Levels of N, P and S ranged from very low to very high (Table 2).

Due to their proximity to the sea, the mean altitude of the NAS was substantially lower than that of the AS. Some NAS were also found on steep banks along creeks and rivers. For the sites located on slopes, there was no association between aspect and fumitory occurrence (Table 1).

Simple relationships between species and environmental variables

The occurrence of all species, except *F. officinalis*, was significantly associated with environmental factors. Because of the

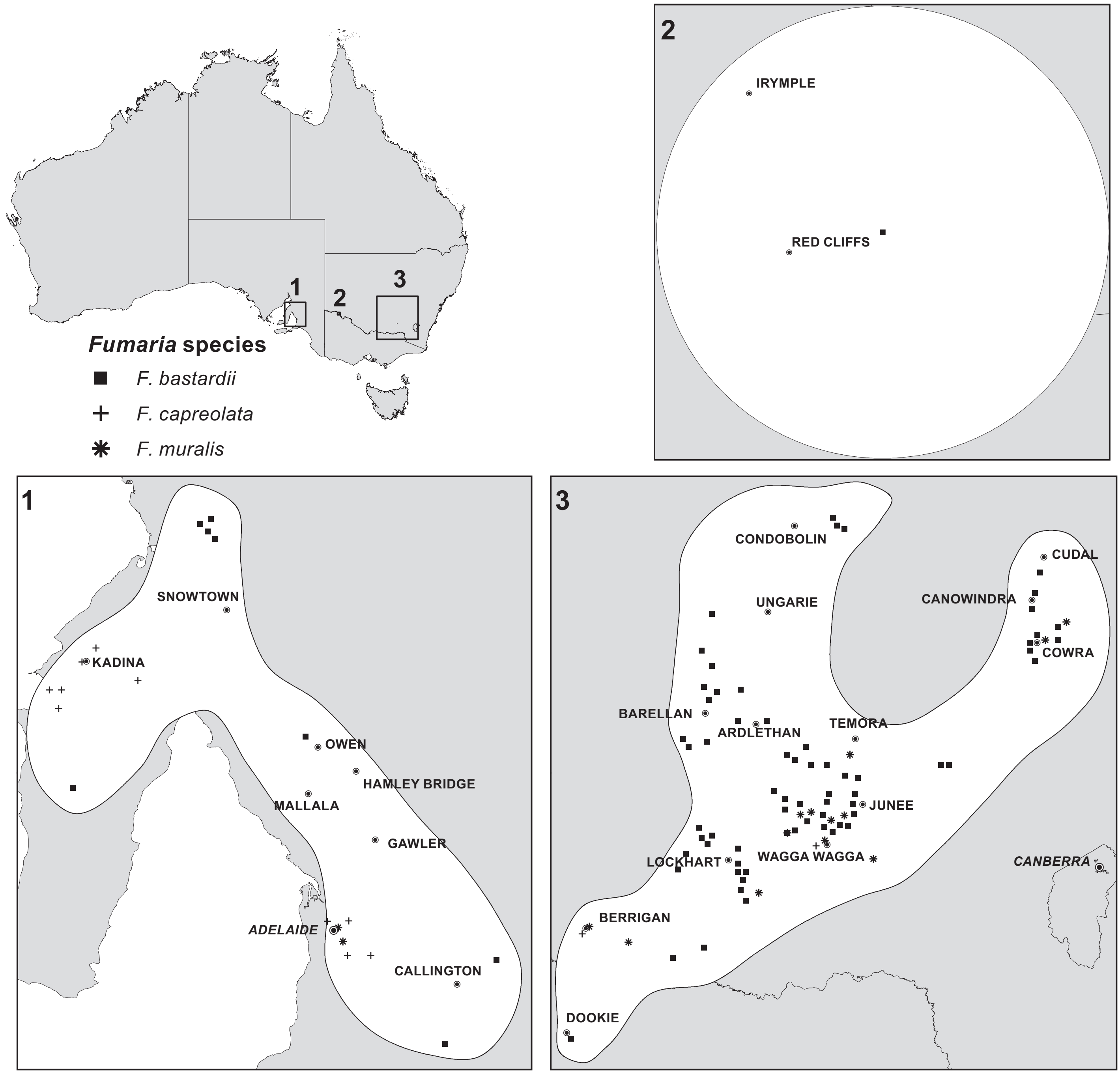

Figure 1 (b). Approximate areas of the survey together with the collection locations in southern New South Wales/northern Victoria and South Australia of the broad-leaved fumitory species *F. bastardii*, *F. muralis* and *F. capreolata*.

non-parametric nature of the distribution functions, all significance levels of χ^2 are given to a probability of 10% (Table 3). The five samples of *F. officinalis* were from environments too heterogeneous for significant associations (Table 3).

Monthly rainfall during the three autumn months was most consistently related to the presence of all five *Fumaria* species. While *F. bastardii*, *F. muralis* and *F. capreolata* showed strong positive relationships with rainfall throughout most of that period, the presence of *F. densiflora* was negatively associated with precipitation in June (Table 3). Conversely, *F. parviflora* was found more often in those areas that receive higher rainfall later in the season.

Fumaria parviflora (χ^2 levels + <0.001 in May and June) and *F. capreolata* (χ^2 levels + <0.001 in June) occurred more often in the warmer parts of the survey area, particularly in South Australian coastal or subcoastal areas. In contrast, *F. bastardii* preferred cooler, more continental environments (χ^2 level − 0.053 in June, Table 3) whereas the occurrence of *F. densiflora* and *F. muralis* was not correlated with temperature.

In all species except *F. bastardii*, significant preferences were found for certain soil texture groups. *F. capreolata* preferred lighter soils (χ^2 level <0.001), *F. muralis* occurred most often in clay-loams (χ^2 level 0.007), while *F. parviflora* was commonly adapted to heavy clay soils, although it could also be present in light soils (χ^2 level <0.001). *F. densiflora* was most often found in either light, sandy loams or light to heavy clays, but there were high probabilities of it occurring in any soil, reflecting the wide-spread distribution of this species (Table 3).

Among the five *Fumaria* species, *F. parviflora* and *F. capreolata* were most associated with soil chemistry variables, indicating more specialized requirements than the other three species. The occurrence of these species was positively correlated with pH, Ca, the presence of limestone, ECEC and all or most macro-nutrient cations, as well as with total C and N, but negatively with Al and Mn (Table 3). However, while higher levels of K in absolute terms seemed to be preferred, these had to be balanced by a simultaneous increase in all other macro-nutrients, particularly Ca, as the correlation with K as a percentage of the ECEC was negative for both species (Table 3). The other three species showed far fewer and usually weaker associations with the soil chemical variables.

The distributions of *F. densiflora* and *F. muralis* were significantly associated with latitude with *F. muralis* found more often in the southern part of the survey zone, while frequency of *F. densiflora* increased toward the north (Table 3).

The presence of all species, except *F. muralis*, was significantly correlated with altitude. *F. densiflora* and *F. bastardii* increased in frequency as altitude increased, whereas the opposite occurred with *F. capreolata* and *F. parviflora*, though only weakly in the case of *F. parviflora* (Table 3).

Table 1. Relative occurrence of each of the categorical environmental descriptors and the frequency of occurrence of *Fumaria* spp. at all survey sites (n = 161), those where agriculture occurred (n=146) and those of a non-agricultural (n = 15) nature.

Variable	All sites (%)	Agricultural sites (%)	Non-agricultural sites (%)
Soil texture group			
Sands	6.2	4.8	20.0
Sandy loams	8.7	6.2	33.3
Loams	13.7	13.7	13.3
Clay loams	14.9	15.7	6.7
Light clays	30.4	32.2	13.3
Medium-heavy clays	26.1	27.4	13.3
Limestone gravel	17.4	12.3	66.7
Rocks	5.0	4.8	6.7
Position in landscape[A]			
Plain	55.8	53.8	73.3
Slope	40.8	43.9	13.3
Valley	2.0	2.3	0.0
River/creek bank	1.4	0.0	13.3
***Fumaria* sp.**			
absent	10.6	11.6	0.0
bastardii	45.3	50.0	6.7
capreolata	6.8	0.0	73.3
densiflora	49.7	54.1	6.7
muralis	9.9	8.2	26.7
officinalis	3.1	3.4	0.0
parviflora	8.7	8.9	6.7

[A] based on n = 147, 132 and 15 for all, agricultural and non-agricultural sites, respectively.

Table 2. Mean (Av.), minimum (Min.) and maximum (Max.) of the continuous environmental variables describing all (n = 161), agricultural (n = 146) and non-agricultural (n = 15) survey sites.

Variable	All sites			Agricultural sites			Non-agricultural sites		
	Min.	Av.	Max.	Min.	Av.	Max.	Min.	Av.	Max.
Latitude (°S)	32.95	34.49	36.37	32.95	34.48	36.37	33.92	34.63	35.67
Altitude (m N.N.)	15	208	565	21	216	565	15	128.2	400.0
Annual rainfall (mm)	300.5	514.9	1095	325.7	514.1	736.6	300.5	522.6	1095
April rainfall (mm)	22.1	41.4	84.5	23.6	41.4	60.3	22.1	41.0	84.5
May rainfall (mm)	27.4	49.6	117.0	27.4	49.0	69.6	29.8	54.9	117.0
June rainfall (mm)	24.1	41.4	143.3	26.9	39.7	75.1	24.1	58.4	143.3
April temp. (°C)	13.8	16.8	18.0	14.6	16.8	18.0	13.8	16.9	17.6
May temp. (°C)	10.9	12.7	14.5	10.9	12.6	14.5	10.9	13.3	14.5
June temp. (°C)	8.0	9.7	12.1	8.0	9.6	12.0	8.6	10.6	12.1
pH	4.10	5.73	8.19	4.10	5.58	7.89	4.52	7.18	8.19
EC (dS m^{-1})	0.04	0.15	0.89	0.04	0.13	0.89	0.12	0.31	0.66
C (%)	0.37	2.10	8.16	0.37	1.86	6.10	1.32	4.39	8.16
N (%)	0.03	0.16	0.41	0.03	0.15	0.39	0.09	0.25	0.41
S (%)	0.00	0.02	0.38	0.00	0.02	0.20	0.00	0.06	0.38
P (mg kg^{-1})	4	22	110	4	20	78	11	48	110
ECEC (cmol kg^{-1})	1.75	12.4	34.0	1.75	11.4	34.0	7.2	22.2	33.3
Ca (cmol kg^{-1})	1.28	8.92	29.2	1.28	8.11	29.2	4.61	16.8	26.6
Mg (cmol kg^{-1})	0.23	1.80	6.12	0.23	1.68	6.12	0.77	2.96	4.18
Na (cmol kg^{-1})	0.00	0.16	2.25	0.00	0.12	1.46	0.01	0.58	2.25
K (cmol kg^{-1})	0.16	1.38	5.89	0.17	1.34	3.45	0.16	1.80	5.89
Al (cmol kg^{-1})	0.00	0.06	1.00	0.00	0.06	1.00	0.00	0.01	0.07
Mn (cmol kg^{-1})	0.00	0.13	0.64	0.00	0.14	0.64	0.00	0.04	0.24

Table 3. Summary of significant correlations (χ^2) between single environmental descriptors and occurrence of *Fumaria* species in a survey in south-eastern Australia.

Environment descriptor	Agricultural sites (n = 146)				All sites (n = 161)	
	Fumaria bastardii	*Fumaria densiflora*	*Fumaria parviflora*	*Fumaria muralis*	*Fumaria muralis*	*Fumaria capreolata*
Latitude		– <0.001		+ 0.043	+ 0.009	
Altitude	+ 0.047	+ 0.037	– 0.082			–0.004
An. Rainfall	+ 0.004		– 0.006	+ 0.006	+ 0.012	
Rainfall April	+ 0.001		– <0.001	+ 0.016	+ 0.010	
Rainfall May	+ 0.043			+ <0.001	+ 0.003	+ 0.037
Rainfall June		–0.016	+ 0.006	+ 0.048	+ 0.000	+ <0.001
Temp. April	– 0.025		+ 0.013			
Temp. May	– 0.015		+ <0.001			+ 0.004
Temp. June	– 0.053		+ <0.001			+ <0.001
pH			+ <0.001			+ <0.001
EC	– 0.087					+ <0.001
C%			+ 0.008			+ <0.001
N%		–0.100	+ 0.003			+ <0.001
S%					+ 0.011	
P ppm			+ 0.051			+ <0.001
ECEC	– 0.058		+ <0.001			+ <0.001
Ca			+ <0.001			+ <0.001
Mg	– 0.029		+ 0.006	– 0.027		+ 0.003
Na	– 0.017	– 0.024				+ 0.004
K			+ 0.005			+ 0.043
Al			– 0.002			– 0.002
Mn			– 0.004			– <0.001
Ca %ECEC			+ <0.001			+ 0.073
Na %ECEC	– 0.089	– <0.001				+ 0.014
K %ECEC			– <0.001			– 0.005
Al %ECEC			– <0.001			– 0.002
Mn %ECEC			– <0.001			– <0.001
Ca:Na						– 0.014
Ca:K			+ <0.001			+ 0.002
Soil texture		0.010	<0.001	0.016	0.007	<0.001
Limestone	– 0.012		+ <0.001	–0.069		+ <0.001
Semi-shade						+ <0.001
Position						0.004

Relationships between Fumaria *species and multiple environmental variables*

Fumaria bastardii Of all the environmental descriptors, April rainfall remained the only significant predictive variable in the maximal model of the stepwise multiple regressions. Figure 2 illustrates the probability P_{bast} of *F. bastardii* occurring in the survey area as affected by average April rainfall. The mean of the rainfall data is located at the origin and is equivalent to 41.4 mm precipitation (Table 2). Calculation of the odds ratio for $x = 10$, which is $e^{10 \times 0.079} = 2.20$, showed that the odds of *F. bastardii* presence in comparison with its absence more than doubled with each 10 mm increase in average April rainfall.

When relating fitted values to actual responses, it became apparent that in some instances there were regional accumulations of prediction errors of the same type: Due to low April rainfall, *F. bastardii* was predicted to be absent from all South Australian sites, except one. However, *F. bastardii* occurred at seven locations in South Australia. In the Ootha/Trundle area of New South Wales, *F. bastardii* was predicted to occur at each location sampled, but was only found on rocky hilltops. This regional clustering of prediction errors suggests the possibility of substantial heterogeneity of this species.

Fumaria densiflora Latitude and the soil parameters Na as % ECEC, % N and soil texture

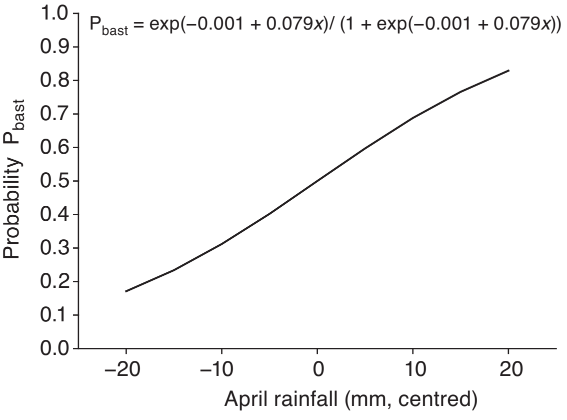

Figure 2. Effect of April rainfall on the probability of *Fumaria bastardii* occurring in the survey area.

were important in their association with the occurrence of *F. densiflora.* The initial maximal model contained the covariates: latitude, altitude, June rainfall, Na, Na as %ECEC, %N and soil texture. The final model only contained the first and last three of these as significant covariates. The probabilities of their respective χ^2-values were <0.001, 0.007, 0.058 and 0.06.

Due to the categorical nature of the variable soil texture, the parameter b_{text} takes different values for the various soil texture groups:

b_{sands} = 0.00
$b_{sandy\ loams}$ = 1.70
b_{loams} = −0.18
$b_{clay\ loams}$ = −0.48
$b_{light\ clays}$ = 1.08
$b_{m/h\ clays}$ = 1.58

From these coefficients, the probability and odds of *F. densiflora* occurring in a certain soil type were calculated for the point where all other variables were held at their mean:

P_{dens} in sands = 0.310, odds = 0.45
P_{dens} in sandy loams = 0.711, odds = 2.46
P_{dens} in loams = 0.273, odds = 0.38
P_{dens} in clay loams = 0.218, odds = 0.28
P_{dens} in light clays = 0.570, odds = 1.33
P_{dens} in m/h clays = 0.686, odds = 2.18

The probability of occurrence of *F. densiflora* at the mean of all other significant covariates was about 2.5 times higher in sandy loams, light clays and medium/heavy clays than in sands, loams and clay loams. The odds of the presence of *F. densiflora* in sandy loams and clays in comparison to its absence in those soils were more than 2:1. In light clays the chances of presence to absence were about equal, and in all other soils less than 0.5:1.

The following parameter estimates and odds ratios were obtained for the continuous variables:

b_{lat} = −0.678 (P of t = 0.019), *OR* = 0.51
$b_{Na\%ECEC}$ = −0.434 (P of t = 0.043), *OR* = 0.65
$b_{N\%}$ = −8.39 (P of t = 0.026), *OR* = 0.00023.

The latitude covariate shows that, independent of soil type, a geographical move south by 1 degree reduced the odds of *F. densiflora* occurring by a factor of 0.51. Similarly, an increase of 1% Na expressed as %ECEC reduced the odds of occurrence by a factor of 0.65, if all other variables were held constant. However, the reduction of odds for each increase of 1% in soil total N% was only by a negligible 0.00023.

There was no regional accumulation of false predictions although half of all occurrences of *F. densiflora* in sandy loam soils came from the Barellan district of New South Wales.

Fumaria parviflora Only limestone presence and soil texture were shown to have a significant effect on the likelihood of occurrence of *F. parviflora* in the multiple regression model. The partial deviance for limestone presence (1 d.f.) was 34.0591 with $P(\chi^2)$ <0.001, and the respective values for soil texture (5 d.f.) were 12.0317 and $P(\chi^2)$ = 0.034.

The presence of limestone dramatically increased the likelihood of occurrence of *F. parviflora* (Table 4) with the odds increasing by a factor of almost 110. In addition, while *F. parviflora* seemed to occur only rarely on medium-textured soils, it was found as commonly in light, sandy soils as on clay soils. This pattern may indicate the existence of different ecotypes within the species.

If a P_{parv} cut-off point of 0.04 for the prediction of presence of *F. parviflora* was applied, the overall prediction error was 3.4%. The low cut-off value reflects the low overall occurrence of *F. parviflora.*

Fumaria muralis Soil texture ($P\chi$ <0.001) and May rainfall ($P\chi$ <0.001) were left as the only covariates significantly correlated with the occurrence of *F. muralis* irrespective of whether analysed with data just from the agricultural sites or whether analysed with data from all sites. These analyses were used to derive probability curves for its occurrence (Figure 3) where the origin represents the mean May rainfall of 49.0 mm in the AS, and the value of 49.9 mm is the mean at all sites.

The extension of the data set to all sites did not substantially affect the coefficient of May rainfall (b_{AS+NAS} = 0.1574 and b_{AS} = 0.1391) and therefore the shape of the regression curves. However, while the curve for AS is only valid in the range between about 25 and 70 mm of May rainfall, the curve for all sites covers a range of up to approximately 120 mm.

Irrespective of whether the site was agricultural, *F. muralis* did not occur much in either very light or very heavy soils (Figure 3). Thus, the resulting probabilities of occurrence were in both cases close to zero across the whole rainfall range (Figure 3). The differences in occurrence between the heavier medium-textured soils were only small in both data sets. However, due to the different distribution of *F. muralis*

Table 4. The probability of occurrence of *Fumaria parviflora* in different soil texture groups with and without the presence of limestone.

Soil texture group	Soil group − limestone	Soil group + limestone
Sands	0.03	0.79
Sandy loams	0.03	0.78
Loams	<0.001	<0.001
Clay loams	<0.001	<0.001
Light clays	0.01	0.53
Medium/heavy clays	0.04	0.81

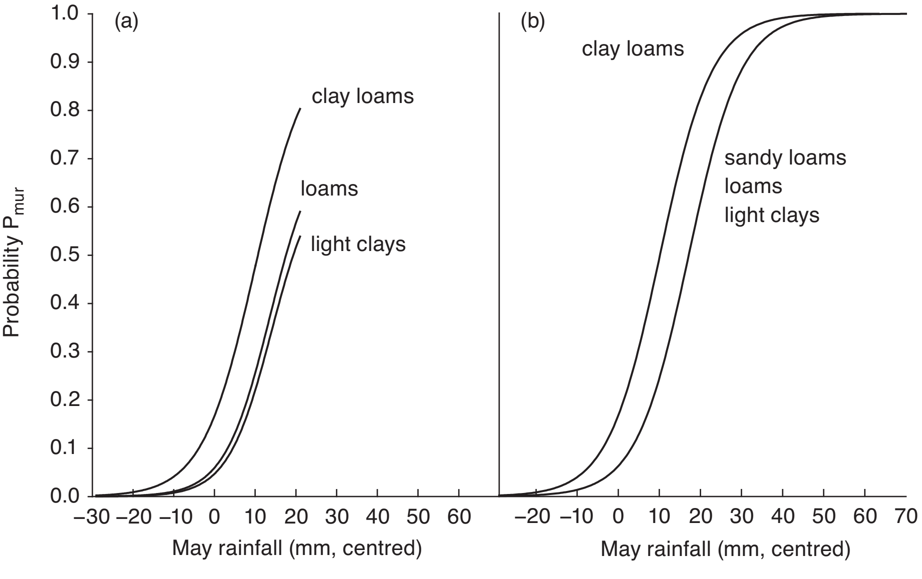

Figure 3. Probability of the presence of *Fumaria muralis* as affected by soil texture and May rainfall at (a) agricultural sites only and (b) at all survey sites.

across the soil texture groups in AS and NAS, a substantial change was seen in the estimate for sandy loams in AS and in that for all sites: While the $b_{sandy\ loams}$ coefficient in agricultural sites is very low (−0.6) and the resulting probabilities predict a near absence of *F. muralis* from those soils in agricultural situations, the probabilities for all sites suggest that it occurs in the same proportions on these soils as on any other of the medium-textured soils (Figure 3). This was entirely due to the lighter soils in the NAS, where *F. muralis* occurred, being characterized by high organic matter.

Calculation of *OR* shows that for each 10 mm increase in May rainfall, the probability of *F. muralis* being present increased by a factor of 4 in the AS, and by a factor of 4.8 when taking all sites into account. The cut-off point of P_{mur} predicting actual presence of *F. muralis* was determined as being P_{mur} ±0.22 in all sites and ±0.21 in agricultural sites with prediction errors being 10.6% and 9.6%, respectively.

Fumaria capreolata The distribution of this species was significantly correlated with the highest number of covariates, suggesting that it might be more specialized in its environmental requirements, than the other species. Fifteen of the more significant, uncorrelated covariates were included in the maximal model: altitude, June rainfall, June temperature, pH, EC, ECEC, %C, mg L^{-1} P, Na, Mg, Mn, Ca:K, K as %ECEC, limestone presence and soil texture. However, due to the low occurrence of *F. capreolata* and the strong association of its presence with specific levels of several covariates, it was not possible to carry out stepwise downward multiple regressions and only the following significant covariates could be fitted in forward multiple regressions: June rainfall ($P\chi < 0.001$), pH ($P\chi < 0.001$), K as %ECEC ($P\chi = 0.003$) and %C ($P\chi = 0.004$). Despite being potentially incomplete, the resulting multiple response curve was highly significant ($P\chi < 0.001$) and predicted presence and absence of *F. capreolata* with an overall error of only 4.3%, where $P_{capr} \geq 0.19$ meant presence and $P_{capr} < 0.19$ meant absence of the species.

The estimated parameters and odds ratios for a one-unit change in the respective *x* value were:

$b_0 = -7.21$
$b_{rainf6} = 0.1387$ ($P_t = 0.008$) *OR* = 1.15
$b_{pH} = 3.69$ ($P_t = 0.02$) *OR* = 39.9
$b_{K\%ECEC} = 0.698$ ($P_t = 0.024$) *OR* = 2.0
$b_{C\%} = 1.127$ ($P_t = 0.018$) *OR* = 3.1

The probability of *F. capreolata* occurring at the mean of all four variables (i.e. at 41.4 mm June rainfall, pH = 5.73, 2.1% total C and K representing 12.8% of the ECEC) was only 0.07%. Consequently, the odds of its presence in comparison to its absence were 0.00073:1. However, these odds were substantially increased by a factor of almost 40 with each unit rise in pH or by 4 for each 10 mm increase in June rainfall, given that all other covariates were held at the same level. *F. capreolata* was usually found in locations with substantially above site-mean values for pH and June rainfall. The shape of the rainfall curve at the mean of all other variables is similar to those presented for *F. muralis*.

Discussion

The six *Fumaria* species studied were not uniformly distributed throughout the survey zone. Indeed the survey has shown their occurrence to be often only regional and influenced by specific edaphic and climatic variables. Soil texture and rainfall during autumn, the germination and early growth period of these species, were the most important variables influencing distribution. Most of these *Fumaria* species, like true agrestal weeds, occurred almost exclusively in regularly disturbed sites. However, others, in particular *F. capreolata*, did not depend on soil disturbance and behaved like true wild plants. Interestingly, Pugsley (1919) concluded that all *Fumaria* species could occur as wild plants in certain natural habitats. Similar to our observations he specifically mentioned *F. capreolata* (1919, 1927, 1932 and 1934) as the species present most frequently in undisturbed sites throughout Europe and Northern Africa. However, *F. capreolata* is also reported to occur in cultivated land in its native range of distribution (e.g. Pugsley 1912, Susplugas *et al*. 1975, Soler 1983).

Fumaria bastardii and *F. densiflora* were the least exacting in their soil texture and rainfall requirement in this survey explaining their widespread and overlapping occurrence. As there are few herbicides capable of controlling *Fumaria* for use in broadleaved crops such as canola, it probably explains why these two species have become important weeds. *F. densiflora* presence was largely unaffected by autumn rainfall amount but more influenced by soil texture, consistent with the report by Pugsley (1912) in Britain, where it occurs either on sandy loams or calcareous clays. Large variability was observed in corolla and sepal size, indicating a heterogeneous species with potentially different bio- and ecotypes. *F. bastardii* was present equally on all soil types, although it occurred more frequently in areas of higher April rainfall. Pugsley (1912) and Stace (1997) report it to occur exclusively in the wetter western part of Great Britain and Ireland, but in Spain it has a much larger rainfall range (Soler 1983, Valdés 1987). Most authors (Pugsley 1912, 1919, Soler 1983) report large morphological variability within *F. bastardii*, which is so marked that some support its division into varieties. This high intra-specific variability may explain the high prediction error rates for this species in parts of the present survey.

The occurrence of *F. muralis*, was significantly affected by both soil texture and rainfall during autumn, most notably during May when it was often flowering. In agricultural sites it preferred the medium to heavier-textured soils with higher rainfall, while in non-agricultural environments it also occurred on lighter soils, provided they were high in organic matter and in higher rainfall areas. This plant is relatively uniform and has more clearly defined moisture requirements than the previous two species. Very high rainfall and very heavy soils do not seem to suit the plant, possibly due to susceptibility to waterlogging as reported by Fedde (1936) and Ellenberg *et al*. (1992) who, with Valdés (1987), state that it mainly occurs on acidic soils, an observation confirmed in the present survey. The soil texture preferences of *F. muralis* make it less likely to occur together with *F. densiflora*, while in higher rainfall areas it is commonly found with *F. bastardii.*

A similar habitat has been described for *F. parviflora*, which suggests it has very specific requirements. For example, Fenni (1993) reports it to be common, sometimes in mass infestations, on calcareous soils in the 300–800 mm rainfall area of northern Algeria. Pugsley (1912) and Stace (1997) found it on the heavy soils of the 'Chalk Districts' of Britain whilst Rauh and Senghas (1976) noted it in the warm, limestone-derived soils of the Rhine and Main valleys in Germany. In Pakistan and India, it is a serious weed of the heavy, calcareous soils of the Punjab (PSSD 1964, Majid and Sandhu 1984, Singh and Singh 1996). In our survey, *F. parviflora* was commonly found in the lime-rich environments, particularly in South Australia and north-western Victoria. The scarcity of these soils in New South Wales explains the rarity of the species in that State. The presence of limestone suggested that the associated pH level is not crucial to species presence, since this varied between 5.1 and 7.8 at *F. parviflora* sites, but rather the high level of Ca as per cent of ECEC, which typically varied between 70 and 85%. This preference for limestone-rich soils makes *F. parviflora* unlikely to accompany *F. bastardii* and *F. muralis* at the same site. If limestone is present, the predilection of *F. parviflora* for sandy as well as heavy soils suggests that it may be a heterogeneous species which is likely to occur together with *F. densiflora* . Indeed, several varieties of *F. parviflora* were described by Pugsley (1919) and, although controversial, the most recent classification of the genus also indicates high variability within this species (Lidén 1986).

In the survey, *F. capreolata* preferred neutral to alkaline, moist and well-draining soils with high levels of organic matter, although there was a scattered, minor occurrence on some slightly acidic soils in New South Wales. Previous descriptions of its habitat refer to neutral to alkaline soils in Mediterranean areas (Susplugas *et al*. 1975, Valdés 1987), whereas populations in Middle Europe seem to be more associated with acidic soils (Ellenberg *et al*. 1992). It was also reported to be present in 'fresh', presumably young or alluvial soils (Valdés 1987, Ellenberg *et al*. 1992) in Europe, or among shady, rocky outcrops in Northern Algeria (Pugsley 1927). Although these descriptions have some commonality with those of the sites where *F. capreolata* was found in Australia, they are not specific enough to explain why *F. capreolata* was not detected in cultivated fields.

Fumaria officinalis was found at only five locations. The populations belonged to three distinct types and it was not possible to identify factors affecting its occurrence. However, the heterogeneity of the species here reflects its widespread distribution in Europe (e.g. Haussknecht 1873, Pugsley 1912, 1919) where it is the most common species, occurring in a very wide range of different climatic environments (Lidén 1986). Closer analysis of its European distribution shows that it primarily occurs in areas with young, relatively unweathered and therefore base-rich soils. Although not clear why it is rare in Australia it is possible that the mostly old, weathered and comparatively infertile Australian soils do not meet its requirements.

Although soil texture and rainfall, as well as pH in some cases, were the most important variables affecting the occurrence of the different species, there were also several 'sporadic' variables. Soil Na content remained a significant, negatively correlated predictor in the multiple regression model for *F. densiflora* and *F. bastardii*, but was positively correlated with the presence of *F. capreolata*. While not explicitly reporting Na levels, Ellenberg *et al*. (1992) support the present findings for *F. bastardii* and *F. densiflora* by categorizing all *Fumaria* species as salt sensitive. Notwithstanding, the range of Na levels detected in the survey sites did not reach levels that are normally considered toxic or growth-inhibiting to crops (Shaw 1985, 1999).

Latitude was an important variable in the model for *F. densiflora*. The attempt to clarify the reason for the importance of latitude, by correlating this with several other environmental variables, was unsuccessful.

It could be hypothesized that the results of this survey indicate that many parts of the south-eastern cropping zone are suitable for colonization by at least one *Fumaria* species, most likely *F. bastardii* and *F. densiflora*. The substantially greater error in predicting the presence of these two species may indicate less specificity in natural environmental requirements and the existence of different ecotypes with as yet incomplete distribution across all suitable habitats. Therefore, further spread into areas presently unaffected by *Fumaria* might be expected. However, the higher prediction error could also mean that factors other than those relating to the natural environment play a role in species distribution. As could be expected in all introduced species, these are likely to include historical chance events which allowed accidental introduction into one area but not another.

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