CHAPTER 6

Predicting the weed-free proportion of the field area with Taylor's power law*

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Summary

Crop weeds are patchily distributed. In weed management it is important to be able to estimate the weed-free fraction of the total field area, because this fraction determines the potential saving on herbicides that may be achieved by site-specific application (and not spraying those patches with no weeds). In this chapter, we model the weed-free fraction by combining Taylor's power law (TPL) for the variance-mean relationship with a prediction of the zero class frequency according to the negative binomial distribution. The resulting predictions of occupancy were compared to observations on weed density and occupancy in 32 data sets on occurrence of agricultural weeds in The Netherlands. The results using weed species specific parameters for TPL provided strong validation for the approach, with $R^2_{\text{prediction}}$ varying between 0.735 and 0.998 for 13 of the 14 species groups. Estimates of the slope parameter *b* of TPL varied substantially between weeds (from 0.78 for volunteer potatoes to 1.95 for *Echinochloa crus-galli*), but only slightly between data sets. Predictions based on a common slope parameter still had high coefficients of prediction for most weed species. Based upon a spatially explicit data set collected using counts in contiguous quadrats, the effect of scale of the sample unit was analysed. At levels of scale relevant to decision making in weed management, the effect of scale on occupancy was minor. We conclude that the relationship between density and occupancy for arable weeds is strong, and that there is scope for prediction of the weed-free area and prediction-based weed management.

Keywords: Taylor's power law, negative binomial distribution, site-specific weed management.

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INTRODUCTION

Weeds tend to occur spatially aggregated on arable land (Marshall, 1988; Wilson & Brain, 1991; Cardina *et al*., 1995; Johnson *et al*., 1995a, b), thus, offering scope for site-specific weed management (Christensen *et al*., 1999). Costs and environmental impact can be reduced by adjusting herbicide application and dosage to weed occurrence and density. Aggregation of weeds can be assessed by examining the frequency distribution of numbers per spatial unit, e.g. a square meter. The negative binomial distribution (NBD) can often be used to describe the frequency distribution of weed counts (Marshall, 1988; Berti *et al*., 1992; Mortensen *et al*., 1992; Wiles *et al*., 1992; Johnson *et al*., 1996a). Its parameter k is an indicator of aggregation, with large values indicating randomness and small values indicating aggregation. The NBD can also be used to calculate the frequency of empty quadrat counts. For site-specific management the unoccupied fraction gives the minimum potential herbicide savings. Potential saving can be even greater if sprays are only applied when weed density exceeds a threshold. Parameter k depends on the mean weed count (abundance). In practice, the mean will generally be observation specific, so k will vary too. The weed-free fraction (which is 1 – occupancy) can be calculated without fitting the NBD if the relation between variance and sample mean has been established. For the mean-variance relationship Taylor's power law (Taylor, 1961) was chosen. Linking the model on mean and occupancy (NBD) with a model describing the relation between the mean and its variance was tested by He & Gaston (2003) on various species such as ticks, beetles and pine trees. Usefulness of the proposed model was further illustrated for distribution of arthropod species on the Azores (Gaston *et al*., 2006).

Taylor's power law (TPL) (Taylor, 1961, 1984) characterizes the relationship between variance and mean for many organisms: $\sigma^2 = a\mu^b$. Parameters a and b are thought of as being characteristic to the species and the scale of sampling (Taylor, 1961; Binns *et al*., 2000). Parameter b is considered an indicator for aggregation of the species at hand, with values > 1 representing aggregation. Parameter a is considered a scale factor. TPL has found wide application in animal ecology such as entomological research for IPM (Binns & Nyrop, 1992; Binns *et al*., 2000). The use of TPL in plant ecology and in particular weed ecology has – so far – been limited (Clark *et al*., 1996). TPL has proved useful in seed bank studies (Dessaint *et al*., 1996; Ambrosio *et al*., 1997) and weed plants (Berti *et al*., 1992) to optimize sampling schemes. Clark *et al*. (1996) examined the effect of scale on parameters a and b, and found that although sample size and spatial scale affected values of parameter a and b, the effects were unpredictable.

We will investigate if the proportion of weed-free area can be predicted from weed density and spatial variance. Furthermore, we will examine the specificity of the relations found and inquire how knowledge on weed-free fraction can be used in weed management. In a second part of the study the effect of scale of observation on level of occupancy will be studied for a detailed spatially explicit data set. Besides scale of the observation quadrats, the effect of the orientation of quadrats on the observed level of occupancy will be looked at.

MATERIALS AND METHODS

Data

Data were collected by Applied Plant Research, The Netherlands, as part of its herbicide efficacy trials (Table 1). A total of 32 data sets were collected between 1995 and 2002, at seven sites (Figure 1), with varying field histories, treatments, soil type, crop, quadrat size and time of observation. All weed counts used in this study were gathered in spring just prior to herbicide spraying. Number of plants per weed species was counted in quadrats, which were evenly distributed over the sampled area.

Additionally, weed count data prior to herbicide spraying were collected in contiguous quadrats over three years (2001, 2002, 2003) in a single field (Kortenoord II) on clay soil cropped with maize in Wageningen (location see Figure 1). These data were used to investigate the effect of size and shape of sample units on the weed-free fraction. The total area sampled with contiguous quadrats was 12 m wide and 50.25 m long. Each quadrat measured 0.75 m × 0.75 m. For full description see Heijting *et al.* (2007).

Analysis: Descriptive statistics and Taylor's power law

Descriptive statistics, including sample mean, variance, minimum, maximum, observed fraction of empty quadrats ($P(0)$) were calculated per weed species for all the data sets. TPL was fitted to the pairs of $^{10}\log$(sample mean) and $^{10}\log$(variance) of all data using linear regression (GENSTAT 8.1, Lawes Agricultural Trust, UK) and Weighted Least Squares (WLS) with number of quadrat count as weight. The results of this will be regarded as the general model or the null model (M_0). In a next step, species specificity of the intercept (log a) or slope (b) was examined by adding species as a factor to M_0, leading to M_a or M_b. Each species is regarded as a factor level (=14). Only weed species which occurred in at least 4 data sets were included in the analysis. The specificity of both parameter a and b was investigated simultaneously in a final step, leading to M_{a+b}. To determine a possible influence of data sets on the resulting model parameters, data sets were added as a factor to the general model. Each data set is a unique combination of year, crop, time of observation, field history, soil type, number of quadrat counts and size of quadrats used. The total number of data sets did

Table 1. Information on data sets: crop, soil type, geographic location, year, field and quadrat size, number of quadrats used and number of main weed species detected.

Observation code	Crop	Soil	Location	Year	Field size	Size quadrat (m^2)	Number of quadrats	Number of main weed species
AGV2347	leek	clay	Lelystad	2001	19.5m×198m	0.75	48	7
AGV3302	onion	clay	Lelystad	2001	19.5m×198m	1.08	40	8
AGV3352	sugar beet	clay	Lelystad	2001	18m×272m	0.3	112	7
AGV4050	sugar beet	clay	Lelystad	2002	18m×268m	0.5	128	11
AGV4051	onion	clay	Lelystad	2002	21m×123m	0.3	108	12
PAV3058	onion	clay	Lelystad	2000	19.5m×200m	0.25	68	5
met1	asparagus	sand	Meterik	2001	15m×48m	0.375	56	3
met2	asparagus	sand	Meterik	2002	15.3m×48m	0.35	56	5
KP480P1E1	fallow	sand	Valthermond	2000	36m×69m	0.8	36	2
KP480P1E2	fallow	sand	Valthermond	2000	36m×69m	0.8	36	2
KP480P2E1	fallow	sand	Valthermond	2000	36m×69m	0.8	36	2
KP480P2E2	fallow	sand	Valthermond	2000	36m×69m	0.8	13	2
KP481P1A	fallow	sand	Valthermond	2000	60m×147m	0.64	108	2
KP481P1B	fallow	sand	Valthermond	2000	60m×147m	0.64	108	2
KP481P2A	fallow	sand	Valthermond	2000	60m×147m	0.64	108	2
KP481P2B	fallow	sand	Valthermond	2000	60m×147m	0.64	32	2
KP500P1E1	fallow	sand	Valthermond	2000	39m×69m	0.64	36	3
KP500P1E2	fallow	sand	Valthermond	2000	39m×69m	0.64	35	3
KP500P2E1	fallow	sand	Valthermond	2000	39m×69m	0.64	36	4
KP500P2E2	fallow	sand	Valthermond	2000	39m×69m	0.64	36	4
KPG216	asparagus	sand	Valthermond	2001	39m×69m	0.25	64	6
PAGV4151AF	maize	sand	Heino	1995	60m×144m	0.75	16	6
PAGV4151BC	maize	send	Heino	1995	60m×144m	0.75	16	5
PAGV4151DE	maize	send	Heino	1995	60m×144m	0.75	16	6
REG3109	maize	sand	Heino	2000	36m×125m	0.5	48	7
PAGV4152AF	maize	sand	Cranendonck	1995	84m×100m	0.75	16	3
PAGV4152BC	maize	sand	Cranendonck	1995	84m×100m	0.75	16	2
PAGV4152DE	maize	sand	Cranendonck	1995	84m×100m	0.75	16	3
VP1008	maize	sand	Vredepeel	2001	97.5m×54m	0.75	120	10
VP1023A	black salsify	sand	Vredepeel	2002	27m×180m	0.15	80	3
VP1023B	black salsify	sand	Vredepeel	2002	27m×180m	0.15	80	3
ZW2369	onion	sandy clay	Colijnsplaat	2001	40.5m×90m	1.08	40	4

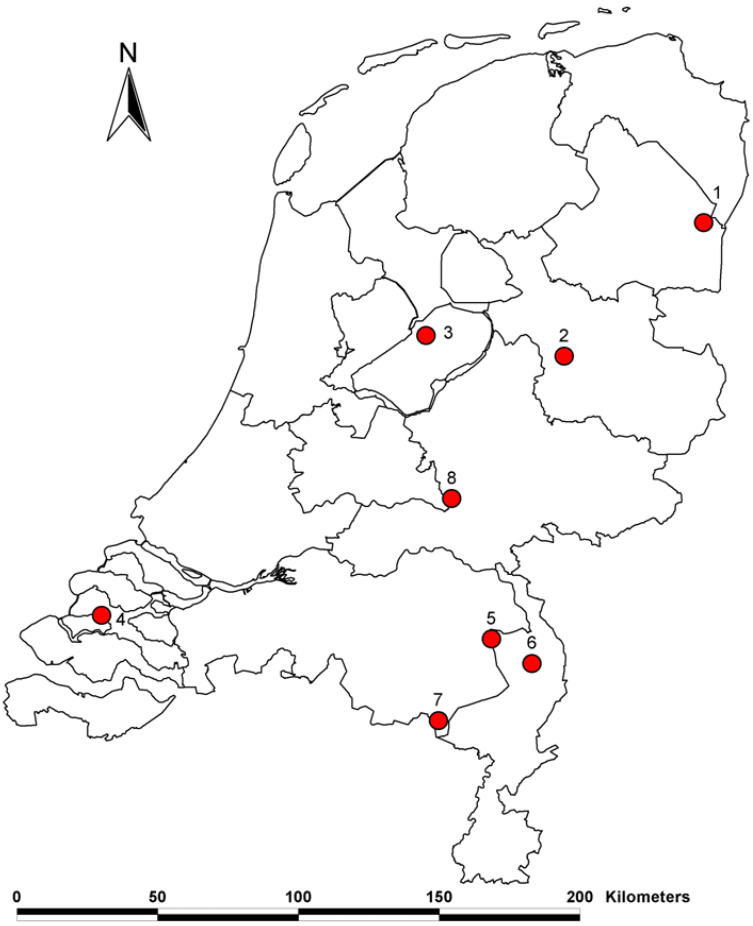

Figure 1. Geographic origins of data sets in The Netherlands: 1. Valthermond, 2. Heino, 3. Lelystad, 4. Colijnsplaat, 5. Vredepeel, 6. Meterik, 7. Cranendonck, 8. Wageningen.

not allow for further analysis on the latter characteristics separately. To ensure the model adequately described Taylor's power law, data sets with 4 or more different weed species were included. R^2_{adjusted} was calculated for all models.

Calculation of weed-free fraction

TPL (Taylor, 1961, 1984) characterizes the relationship between variance and sample mean for organisms following

$$\sigma^2 = a\mu^b \tag{1}$$

The negative binomial distribution has parameter μ and k. The parameter k can be estimated from observed mean and variance as:

$$k = \frac{\mu^2}{\sigma^2 - \mu} \tag{2}$$

The zero class frequency of the negative binomial distribution is:

$$P(0)=\left(\frac{k}{k+\mu}\right)^{k} \tag{3}$$

Equations 1, 2 and 3 can be combined (He & Gaston, 2003; Gaston *et al.*, 2006) to obtain the following equation for calculating the zero class frequency, based on observed mean μ, and parameters *a* and *b* of TPL:

$$P(0)=\left(\frac{1}{a\mu^{b-1}}\right)^{\mu^2/(\sigma^2-\mu)} \tag{4}$$

Expected fraction of weed-free quadrats was calculated for each weed species-data set combination. $R^2_{\text{predicted}}$ (Turchin, 2003) was calculated between calculated and observed weed-free fraction of quadrats to determine the suitability of our approach to calculate the weed-free fraction.

Effect of scale and shape of observation quadrat

Kortenoord II data comprised three subsequent years. To determine the effect of scale and orientation on observed weed-free area fraction, quadrats were aggregated to gain higher level of scale according to the following scheme:

Scale	In-Row	Across-Row
1	1×1	1×1
2	2×1	1×2
3	3×1	1×3
4	4×1	1×4

The sign test ($P<0.05$) was performed to investigate on differences between the two directions (in-row and across-row). The effect of scale and orientation was investigated with Delphi (Delphi, Borland Inc., Scotts Valley, CA, USA).

RESULTS

Prediction of the weed-free fraction of the field

Throughout the data sets, *Chenopodium album*, *Polygonum persicaria*, *Poa annua*, *Stellaria media* and *Solanum nigrum* were the most frequent (Appendix 1) weed species. Fraction of empty quadrats ($P(0)$) varied largely depending on the observation. If counts of all weed species of a data set were summed, this fraction was smaller than 0.1 and often close to zero.

The general regression model M_0 adequately described ($R^2_{\text{adjusted}} = 0.96$) the relation between weed sample mean and its variance, with $^{10}\log a = 0.5160$ and $b = 1.3904$ (Table 2). If species were added as a factor, both slope (*b*) and intercept ($^{10}\log a$)

significantly differed (P<0.05) from the general model. The variance accounted for by the regression changed slightly but significantly when species specificity of both parameters was included in the model ($R^2_{adjusted}$ = 0.97). Addition of data set as a factor to M_0 gave a similar effect as weed species (Table 3). Only 107 data points could be used as not all data sets comprised enough weed species for the regression analysis.

TPL could be fitted to 13 weed species and volunteer potato plants (*Solanum tuberosum)* (Figure 2; Table 4). $R^2_{adjusted}$ for the fitted species specific relationship were high, often above 0.91 with *Senecio vulgaris* attaining the maximum of 1.0. *Solanum tuberosum* was the exception with $R^2_{adjusted}$ = 0.79. The latter weed gave the lowest b (0.78). For all other weed species the value of parameter b was between 1.18 (*Matricaria* spp.) and 1.95 (*Echinochloa crus-galli*). Values of parameter a varied between 1.54 (*S. tuberosum*) and 7.15 (*Polygonum convolvulus*).

Table 2. Details of the general model and species specific models for regression between ^{10}log(mean) and ^{10}log(variance) according to Taylor's power law, ^{10}log(variance) = b × ^{10}log(mean) + ^{10}log(a). Parameter b, ^{10}log(a), their s.e., significances, parameter a and $R^2_{adjusted}$ of the model is presented. The number of data points (N) was 146.

Model	b	s.e.	^{10}log(a)	s.e.	a	R_{adj}^2
M_0: not species specific	1.39	0.02	0.52	0.02	3.28	0.963
M_a: parameter a species specific	1.41	0.03	*see Table 4*			0.966
M_b: parameter b species specific	*see Table 4*		0.48	0.03	3.03	0.964
M_{a+b}: parameter a+b species specific	*see Table 4*					0.97

Table 3. Details of the general model and data set specific models for regression between ^{10}log(mean) and ^{10}log(variance) according to Taylor's power law, ^{10}log(variance) = b × ^{10}log(mean) + ^{10}log(a). Parameter b, ^{10}log(a), their s.e., significances, parameter a and $R^2_{adjusted}$ of the model are presented. The number of data points (N) was 107.

Model	b	s.e.	^{10}log(a)	s.e.	a	R_{adj}^2
M_0: not data set specific	1.35	0.03	0.49	0.03	3.09	0.96
M_a: parameter a data set specific	1.30	0.03	-*			0.966
M_b: parameter b data set specific	-*		0.44	0.03	2.76	0.97
M_{a+b}: parameter a+b data set specific	-*					0.97

* not shown here.

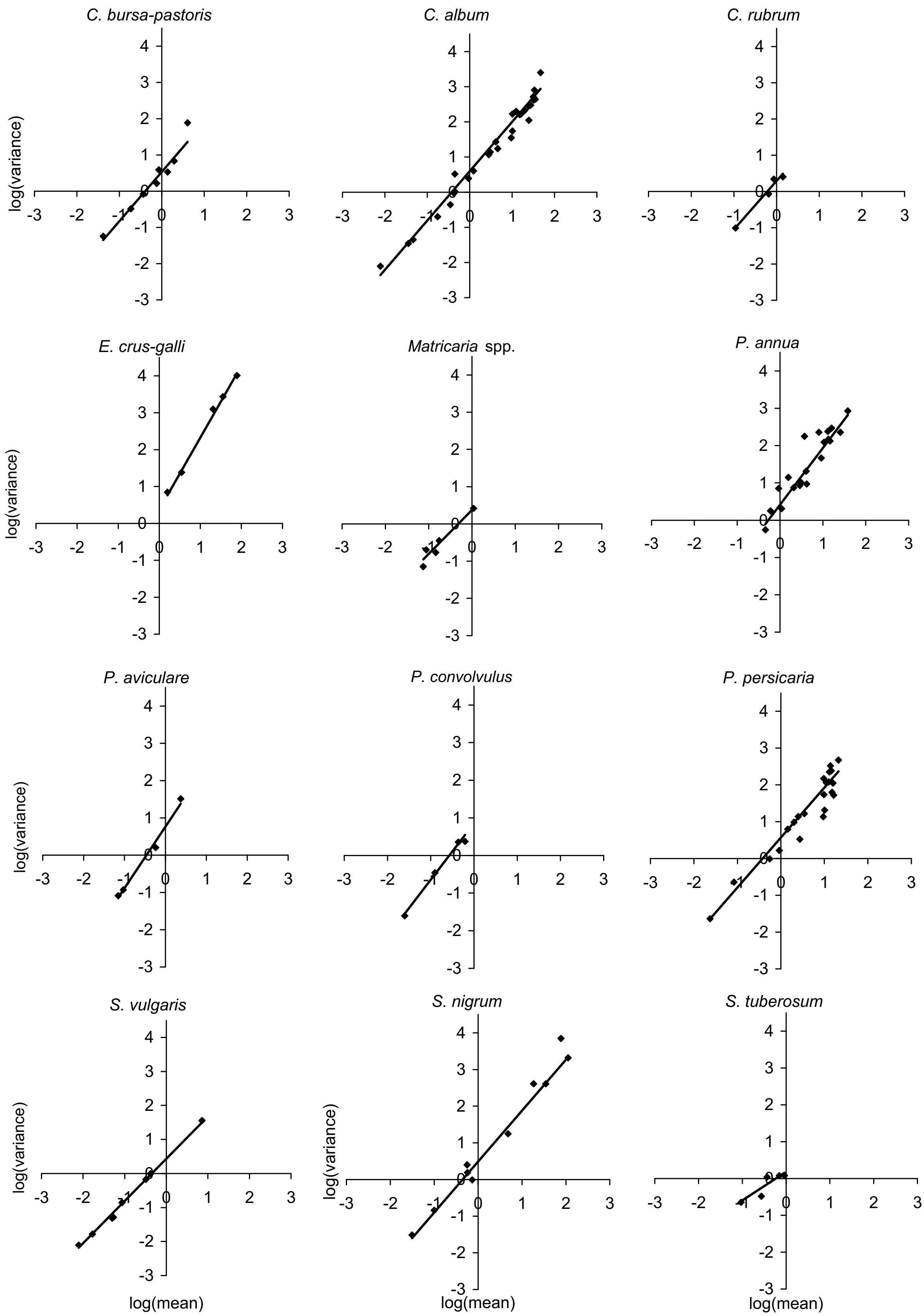

Figure 2. Species-specific results of fitting Taylor's power law.

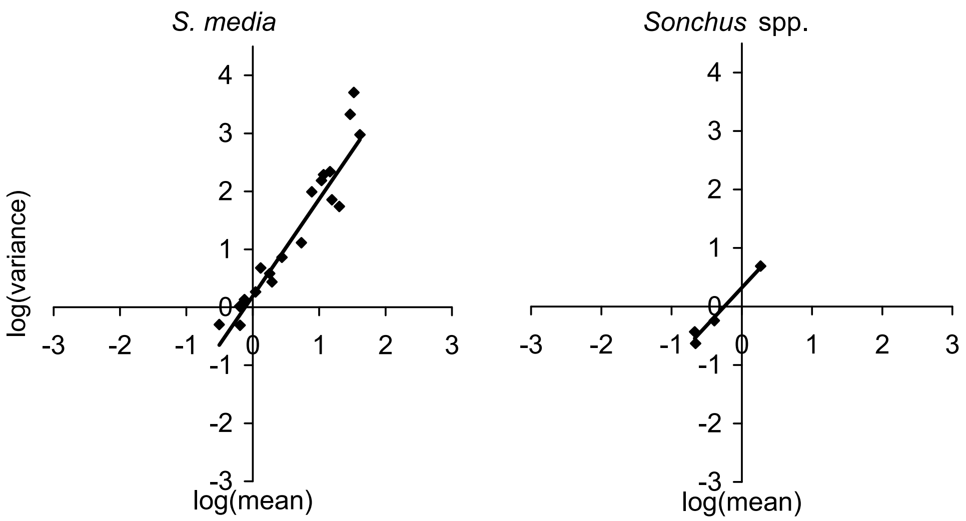

Figure 2. Continued. Species-specific results of fitting Taylor's power law.

Table 4. Results per weed species group for regression between ^{10}log(mean) and ^{10}log(variance) according to Taylor's power law. The parameters b, a, $^{10}\log(a)$ for the model $^{10}\log(\text{variance}) = b \times {}^{10}\log(\text{mean}) + {}^{10}\log(a)$, their s.e., significances and R^2_{adjusted} of the model and number of data sets included (N) are given.

Weed species	b	s.e.	P	$^{10}\log(a)$	s.e.	P	a	R^2	N
C. bursa-pastoris	1.36	0.13	<0.001	0.53	0.09	<0.001	3.42	0.94	8
C. album	1.40	0.03	<0.001	0.60	0.04	<0.001	3.95	0.98	30
C. rubrum	1.34	0.14	0.011	0.29	0.08	0.065	1.95	0.97	4
E. crus-galli	1.95	0.09	<0.001	0.37	0.07	0.015	2.36	0.99	5
Matricaria spp.	1.18	0.15	0.005	0.37	0.12	0.017	2.34	0.94	5
P. annua	1.59	0.12	<0.001	0.32	0.10	0.002	2.07	0.94	18
P. aviculare	1.67	0.15	0.006	0.78	0.12	0.016	5.98	0.98	4
P. convolvulus	1.50	0.11	0.004	0.85	0.11	0.051	7.15	0.98	4
P. persicaria	1.36	0.07	<0.001	0.57	0.07	<0.001	3.73	0.95	22
S. vulgaris	1.24	0.03	<0.001	0.43	0.05	<0.001	2.72	1.00	8
S. nigrum	1.39	0.07	<0.001	0.49	0.08	<0.001	3.08	0.98	10
S. tuberosum	0.78	0.20	0.028	0.19	0.12	0.23	1.54	0.79	5
Sonchus spp.	1.29	0.15	0.013	0.32	0.07	0.049	2.10	0.96	4
S. media	1.67	0.13	<0.001	0.19	0.12	0.113	1.57	0.91	19

Species specific values of parameter *a* and *b* (Appendix 2) were compared ($P<0.05$). Significant differences between weed species were present but weed species could not be grouped accordingly. This is probably caused by the limited number of these data sets. For some weed species only four data sets were available for regression of TPL (Table 4).

Proportion of weed-free quadrats was well predicted (Figure 3; Table 5) for all dicot weed species with values of $R^2_{\text{predicted}}$ between 0.87 (*P. convolvulus*) and nearly 1.0 (*S. vulgaris*). For grass weeds, $R^2_{\text{predicted}}$ had lower values; 0.74 for E. *crus-galli* and 0.37 for *P. annua*. The closer to 1 $R^2_{\text{predicted}}$ lies, the better the model performed in calculating the weed-free fraction. Values near 0 indicate the model did not contribute to a better calculation. And values of $R^2_{\text{predicted}} < 0$ indicate that the calculation with our approach was poorer than using the mean. Using parameter values of the general model for prediction of the calculated weed-free fraction resulted in similar outcomes compared to the species specific model (M_{a+b}) for around half the weed species. For the remaining weed species, the general model gave a poorer performance in calculating the weed-free fraction. For *E. crus-galli* a negative value of $R^2_{\text{predicted}}$ was found, showing that for this weed species the general model was inadequate.

Table 5. Values of $R^2_{\text{predicted}}$ for the prediction of the weed-free fraction according to the species specific models and the general model of Taylor's power law for 14 weed species groups.

	$R^2_{\text{predicted}}$	
Weed species	Species specific model	General model
Capsella bursa-pastoris	0.891	0.895
Chenopodium album	0.976	0.976
Chenopodium rubrum	0.962	0.744
Echinochloa crus-galli	0.735	–0.335
Matricaria spp.	0.976	0.907
Poa annua	0.376	0.451
Polygonum aviculare	0.961	0.831
Polygonum convolvulus	0.868	0.393
Polygonum persicaria	0.954	0.957
Senecio vulgaris	0.998	0.997
Solanum nigrum	0.912	0.910
Solanum tuberosum	0.936	0.726
Sonchus spp.	0.981	0.845
Stellaria media	0.894	0.859

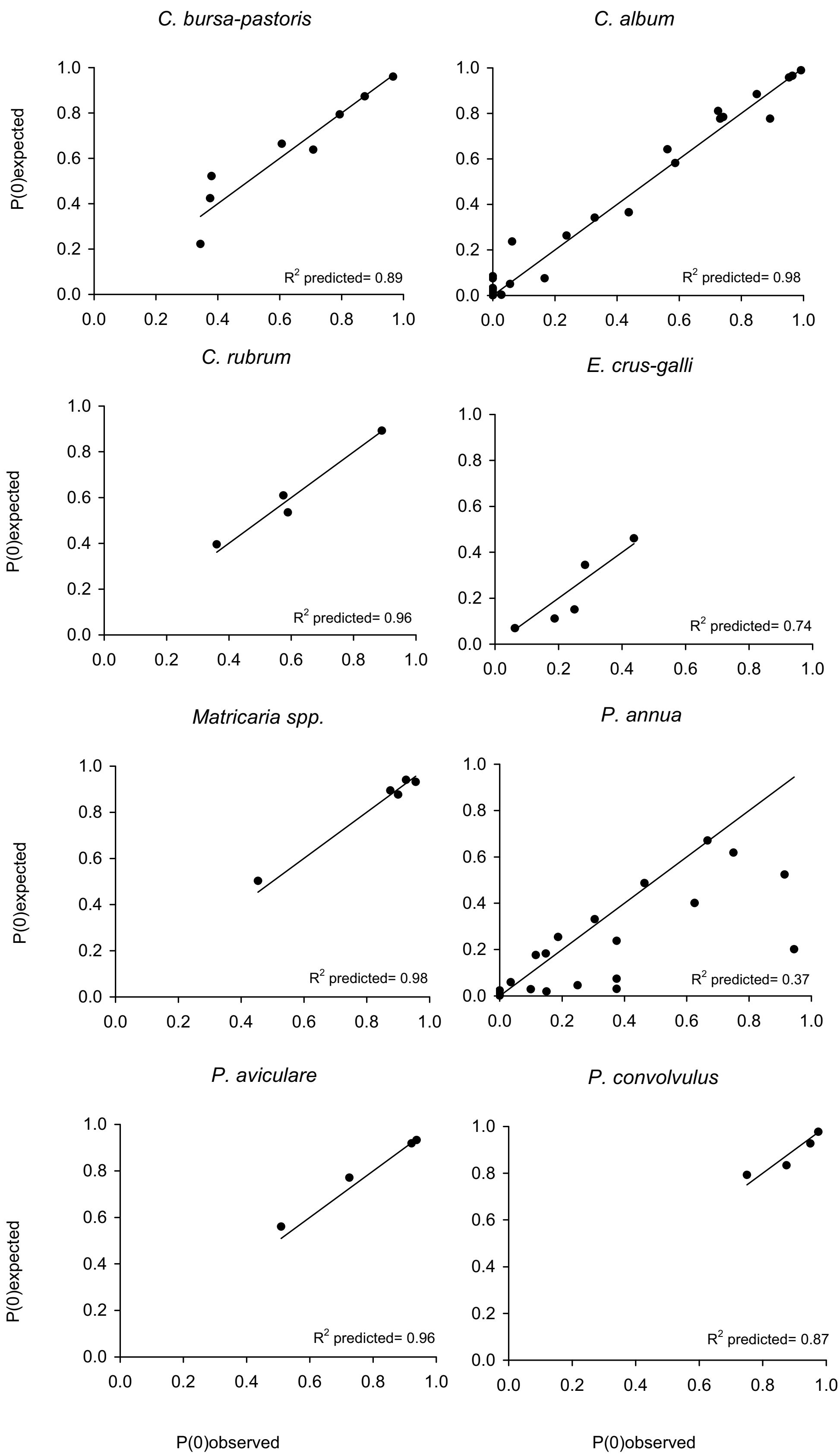

Figure 3. Observed and expected fraction of empty quadrats for 14 weed species groups, according to the species specific model. Each point in the graph represents a data set.

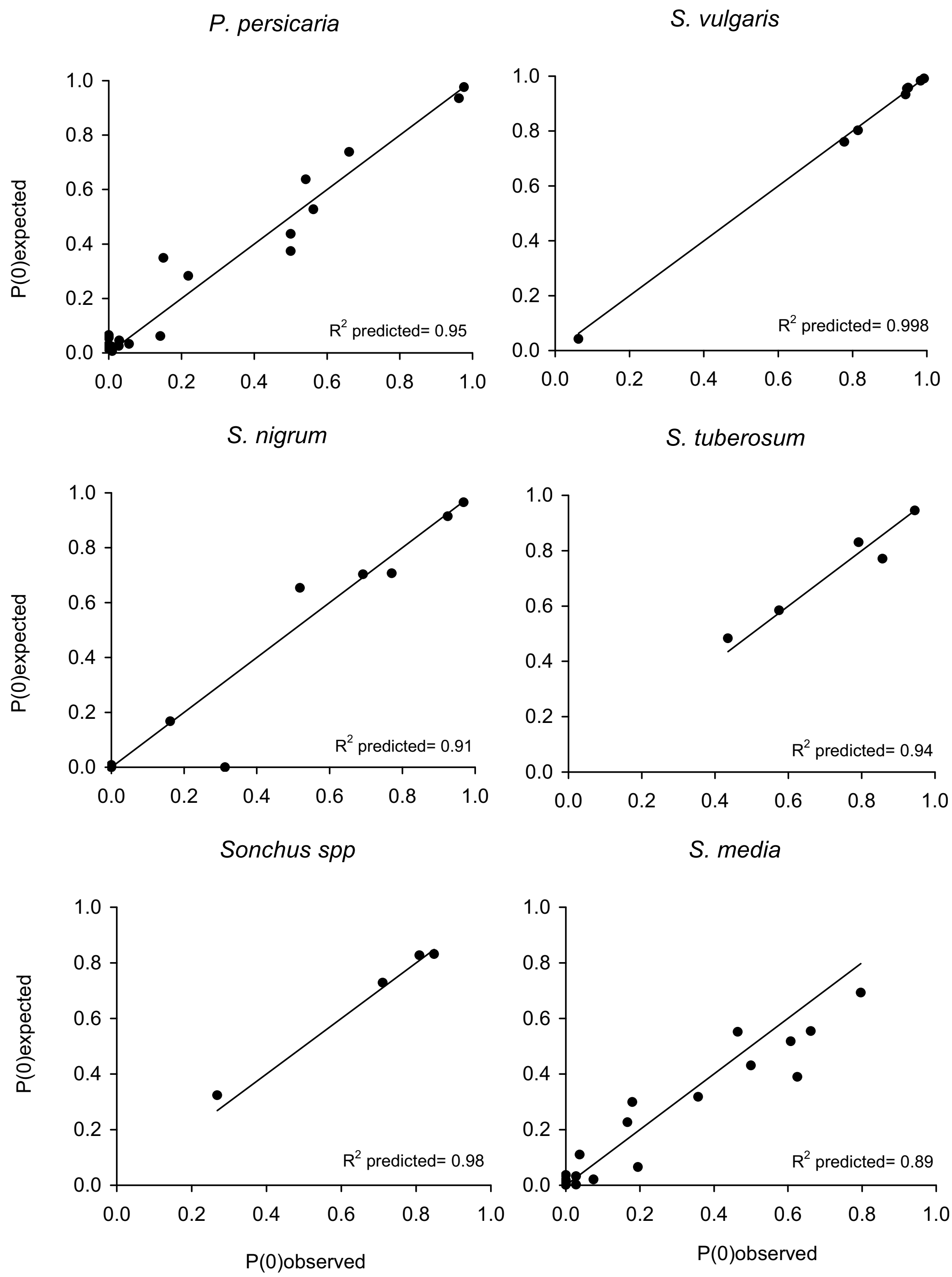

Figure 3. Continued. Observed and expected fraction of empty quadrats for 14 weed species groups, according to the species specific model. Each point in the graph represents a data set

Effect of scale and sample unit on observed fraction of empty quadrats

In Figure 4, the effect of orientation and scaling on observed occupancy fraction is presented for some important weed species. Although the difference between in-row and across-row aggregation was very small, it was significant for scale level 2, with

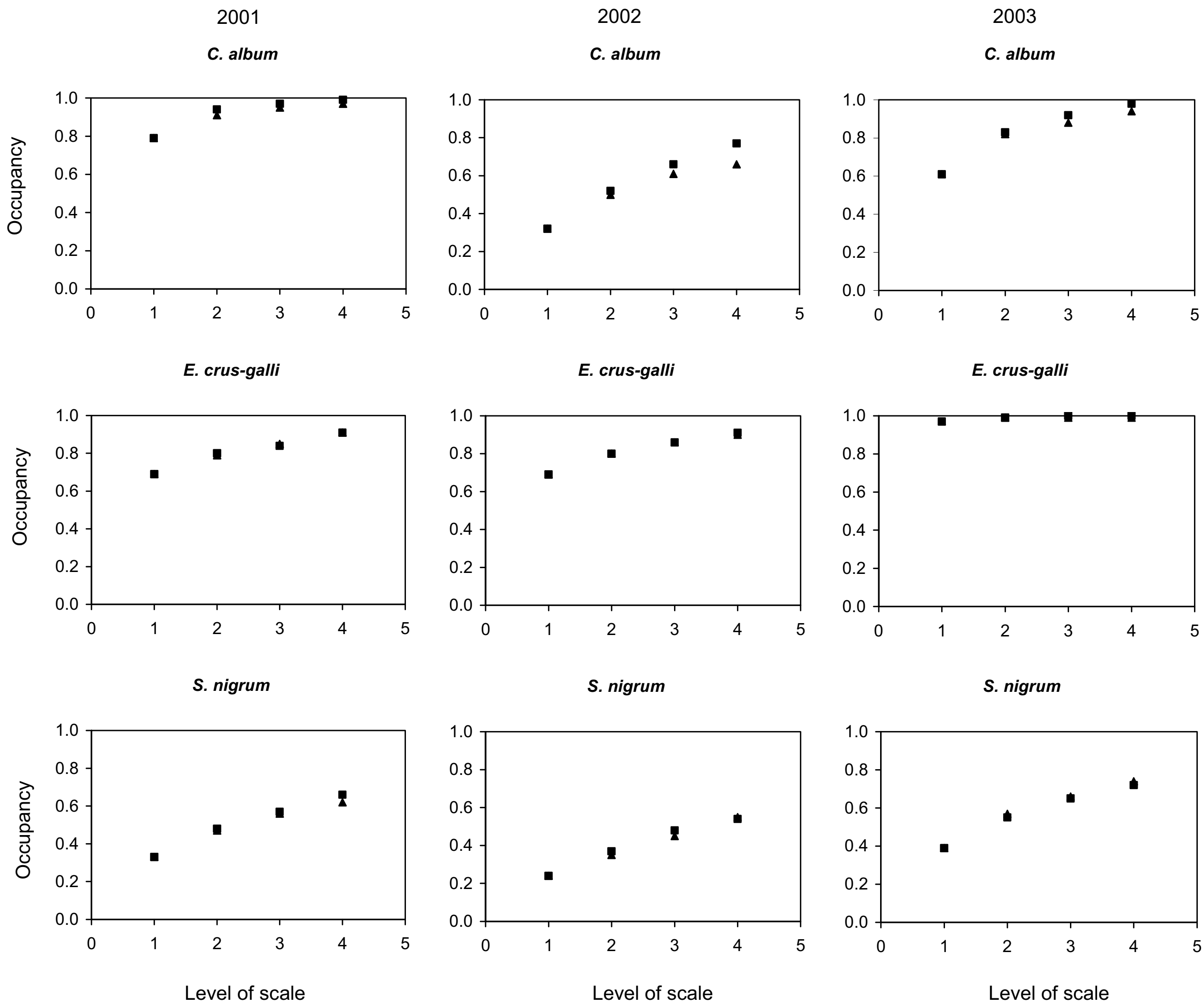

Figure 4. Effect of scale and direction of aggregation on observed occupancy. The two directions are cross-row (▲) and in-row (■).

P(0) for in-row being smaller than across-row aggregation if all 6 examined weed species were regarded simultaneously. For the larger levels of scale, no significant differences occurred.

Aggregation of quadrats in larger observation units resulted in a quick decrease of weed-free fraction (Figure 5).

DISCUSSION

Overall, the weed-free fraction was predicted well using the observed mean density of a weed species combined with the general model of Taylor's power law. Some potentially large savings are possible as for most weed species a significant weed-free fraction was present in the field. However, if the entire weed population is considered, the observed weed-free fraction is often close to zero. Therefore, in practice greatest reductions will be obtained if more than one herbicide is needed to kill most species of the weed population and a second herbicide is applied site-specifically to target the remaining weed species (Gerhards & Christensen, 2003).

The results on clustering quadrats into larger units showed that possible savings are quickly declining with increasing level of scale. This is in line with findings of Rew *et al*. (1997) and Wallinga *et al*. (1998). At one level of scale, aggregation of quadrats in a particular direction in the field did affect the observed weed-free area significantly, although the differences were very small. The presence of anisotropy in most of the observed weed patterns (Heijting *et al*., 2007) could explain this detected significance.

Taylor's power law well described the relation between the sample mean and variance of the weed counts in this study, as it previously did for many other organisms (Taylor *et al*., 1978) and weed plants (Berti *et al*., 1992; Clark *et al*., 1996). The parameter values for the slope and intercept of our general model (s^2=0.52+1.39m) were similar to those reported by Dessaint *et al*. (1996) for their general model for weed seeds in the seed bank (s^2=0.45+1.41m). Only for a few weed species the general model did not give an adequate prediction of the weed-free fraction and species specific parameters of Taylor's power law were required to obtain satisfactory output. Species specificity was significantly present in our study for both parameter a and b,

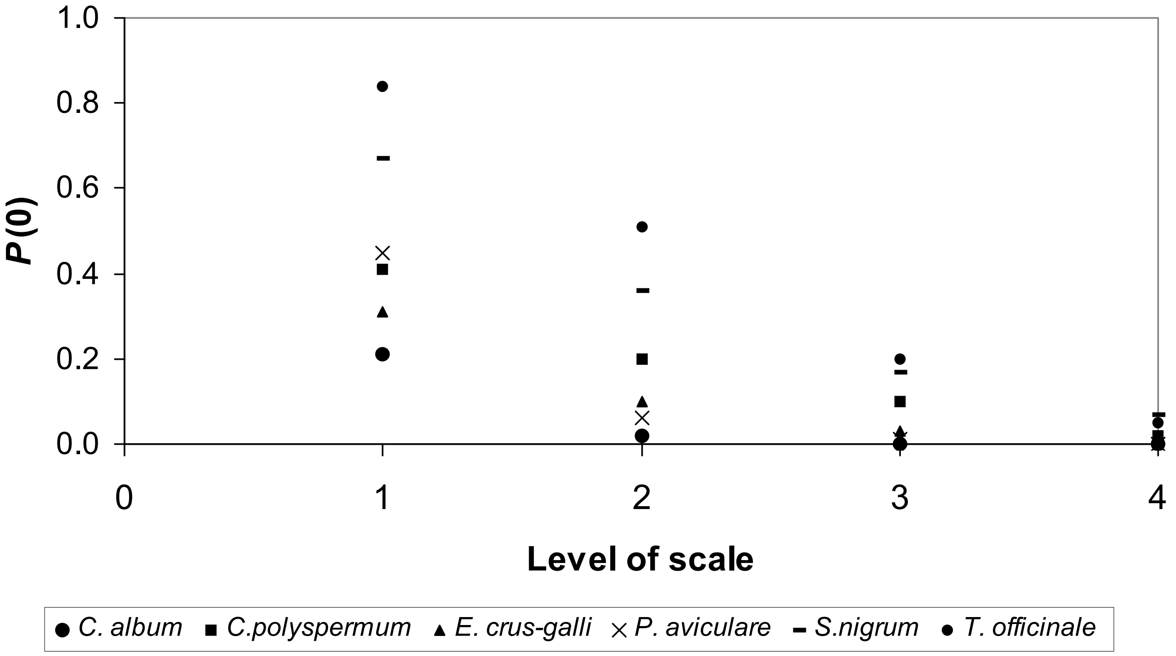

Figure 5. Fraction weed-free area ($P(0)$) as a function of scale for six weeds species on Kortenoord II 2001.

though no clear groups of weeds emerged from the significances found. This was probably caused by the limited number of variance/mean pairs in the regression analysis of some species. Species specific values for the two parameters of TPL were not found in other studies on weed plants (Berti *et al*., 1992; Clark *et al*., 1996) or weed seeds. Berti *et al*. (1992) reported that although in the overall regression no species specificity could be traced, some weed species emerged as locally significant weed species. It will be interesting to know if species specificity will filter out if weed counts have been gained under a very wide range of circumstances. The importance of extensive data for species specificity was been pointed out (Taylor *et al*., 1988) as it will be difficult, if not impossible to keep conditions equal if various locations are examined.

The values we found for parameter *b* [0.78–1.95] coincided largely with the range indicated by Taylor *et al*. (1978) for plant species [0.82–1.48]. As Clark *et al*. (1996) pointed out, the range is expected to grow with an increasing number of plant species examined. *E. crus-galli* had the steepest slope of TPL (1.95). Volunteer potato (*S. tuberosum*) was the only species in our study with a slope < 1 (0.78) which most likely reflects the regular pattern in which the potatoes were planted in previous years. All other weed species in this study had slopes above 1.18, indicating some form of spatial aggregation. Wiles *et al*. (1992) mentioned that possible savings will depend on the spatial configuration of the weeds. Less advanced technological equipment is needed in the field if weeds are strongly positively correlated and have spatially aggregated patterns.

Besides species, data set as a factor had a slight but significant effect on the parameter outcome of Taylor's power law. Each data set comprised a combination of geographic location, field history, soil type, quadrat size and number, time of observation and crop, and any (combination of) these factors could have contributed to differences in TPL parameters. All these are known to affect the results found when fitting TPL. Berti *et al*. (1992) found that crop type, winter versus summer, significantly affected the outcomes of the parameter values. Mulugeta & Boerboom (1999) showed that differences in spatial aggregation existed between cohorts of the same weed population and these differences were reflected in parameter values of TPL.

The least good prediction of weed-free fraction, as indicated by $R^2_{\text{predicted}}$, was obtained for the two grass weed species that occurred in the data sets. A possible reason could be that with counting grass-weed plants it is more difficult to distinguish between individuals than for dicot weeds, which results in more inaccurate counts.

Besides its application to calculate weed-free area, knowledge on parameters of TPL for weeds can help for modelling on crop yield loss by weed densities (Clark *et al*., 1996), and weed sampling programmes (Berti *et al*., 1992; Dessaint *et al*., 1996).

Furthermore, relations between environmental covariates and spatial patterns of organisms can be examined using TPL as was shown for insect larvae and organic matter by Dalthorp (2004). This approach was recently successfully applied to weed spatial patterns and soil characteristics (Heijting *et al*., 2005).

CONCLUSIONS

The weed-free fraction can be modelled by linking a model for the spatial variance with a model for the frequency distribution of weed counts, i.c. Taylor's power law (TPL), and the Negative Binomial Distribution. Predominant weed species throughout the spatial implicit data sets were *C. album*, *P. annua*, *P. persicaria*, *S. media* and *S. nigrum*. The weed-free fraction of the total weed population was approximately between zero and 0.1.

Using the general model of Taylor's power law to predict weed-free fraction gave similar results as the species specific models for the majority of the fourteen weed species examined here. The results show that the proposed model provides a valid tool for predicting occupancy in weeds.

Orientation of quadrats affected the total weed-free area at the lowest level of aggregation. This was caused by a stronger correlation in-row direction than cross-row. Clustering quadrats to higher scale levels resulted in a quick decrease in weed-free area.

Appendix 1

Summary statistics for 32 data sets. Mean, variance, minimum, maximum are expressed in number per quadrat. *P*(0)observed indicates fraction of empty quadrats of total number of quadrats. Rare weed species are omitted.

Data set	Weed species	mean	variance	min.	max.	*P*(0)observed
AGV2347	*C. bursa-pastoris*	0.19	0.33	0	3	0.88
	Matricaria spp.	0.15	0.17	0	2	0.88
	P. annua	0.46	0.55	0	3	0.67
	S. vulgaris	7.25	36.23	0	32	0.06
	S. nigrum	0.56	2.51	0	10	0.77
	S. tuberosum	0.27	0.33	0	2	0.79
	S. media	2.75	7.30	0	10	0.17
	Total weeds	11.63	42.96	0	34	0.04
AGV3302	*C. album*	0.18	0.20	0	2	0.85
	C. rubrum	0.65	0.85	0	3	0.58
	Matricaria spp.	0.08	0.07	0	1	0.93
	P. annua	0.60	1.78	0	6	0.75
	S. vulgaris	0.05	0.05	0	1	0.95
	S. nigrum	0.10	0.14	0	2	0.93
	S. tuberosum	0.70	1.19	0	4	0.58
	S. media	1.10	1.84	0	5	0.50
	Total weeds	3.45	5.28	0	11	0.08
AGV3352	*C. bursa-pastoris*	0.76	1.64	0	6	0.61
	C. album	0.04	0.03	0	1	0.96
	C. rubrum	0.87	2.19	0	9	0.59
	P. annua	4.21	9.32	0	14	0.12
	Sonchus spp.	0.21	0.37	0	4	0.85
	S. tuberosum	0.37	1.10	0	5	0.86
	S. media	1.79	3.82	0	9	0.36
	Total weeds	8.24	26.98	0	22	0.04
AGV4050	*C. album*	0.01	0.01	0	1	0.99
	C. rubrum	0.11	0.10	0	1	0.89
	C. bursa-pastoris	1.96	6.81	0	12	0.38
	P. annua	2.09	7.45	0	16	0.30
	P. aviculare	0.07	0.08	0	2	0.94
	P. persicaria	0.02	0.02	0	1	0.98
	S. vulgaris	0.01	0.01	0	1	0.99
	Sonchus spp.	0.41	0.57	0	4	0.71
	S. nigrum	0.03	0.03	0	1	0.97
	S. tuberosum	0.09	0.23	0	4	0.95
	S. media	1.95	2.74	0	8	0.18
	Total weeds	6.75	14.05	0	19	0.01

Data set	Weed species	mean	variance	min.	max.	$P(0)$observed
AGV4051	*C. album*	0.05	0.04	0	1	0.95
	C. rubrum	1.41	2.54	0	6	0.36
	C. bursa-pastoris	1.37	3.41	0	9	0.38
	P. annua	4.06	20.57	0	23	0.15
	P. aviculare	2.36	32.53	0	34	0.51
	P. persicaria	0.08	0.23	0	4	0.96
	Matricaria spp.	1.09	2.61	0	10	0.45
	S. vulgaris	0.32	0.67	0	5	0.81
	Sonchus spp.	1.85	4.89	0	16	0.27
	S. nigrum	0.73	0.98	0	4	0.52
	S. tuberosum	0.92	1.20	0	5	0.44
	S. media	20.18	54.97	5	43	0.00
	Total weeds	34.43	140.43	19	71	0.00
met1	*C. album*	0.45	3.27	0	10	0.89
	P. annua	1.09	2.05	0	6	0.46
	S. media	0.75	1.35	0	5	0.61
	Total weeds	2.29	4.86	0	11	0.16
met2	*C. album*	0.45	1.05	0	5	0.73
	P. persicaria	0.55	0.98	0	5	0.66
	P. annua	9.20	46.63	0	29	0.04
	S. vulgaris	0.05	0.05	0	1	0.95
	S. media	0.64	0.49	0	3	0.46
	Total weeds	10.89	47.92	1	29	0.00
KP480P1A	*C. album*	10.19	168.16	0	54	0.17
	P. persicaria	9.75	54.31	1	40	0.00
	Total weeds	19.94	209.77	2	65	0.00
KP480P1B	*C. album*	12.42	199.62	0	66	0.06
	P. persicaria	15.03	62.66	1	43	0.00
	Total weeds	27.44	227.51	5	77	0.00
KP480P2A	*C. album*	15.06	161.00	1	52	0.00
	P. persicaria	16.37	52.36	8	42	0.00
	Total weeds	31.43	184.25	12	67	0.00
KP480P2B	*C. album*	9.54	35.44	5	27	0.00
	P. persicaria	10.15	20.64	3	20	0.00
	Total weeds	19.69	78.23	13	47	0.00
KP481P1A	*C. album*	33.53	806.42	2	157	0.00
	P. persicaria	14.48	242.42	0	89	0.01
	Total weeds	48.01	1264.27	5	198	0.00
KP481P2A	*C. album*	24.31	277.60	1	85	0.00
	P. persicaria	15.79	111.29	0	49	0.01
	Total weeds	40.10	411.31	11	103	0.00
KP481P1B	*C. album*	46.62	2513.83	3	414	0.00
	P. persicaria	21.06	471.82	0	128	0.01
	Total weeds	67.69	3342.69	5	458	0.00
KP481P2B	*C. album*	16.09	166.54	1	60	0.00
	P. persicaria	9.44	13.61	3	18	0.00
	Total weeds	25.53	156.19	11	69	0.00

Data set	Weed species	mean	variance	min.	max.	*P*(0)observed
KP500P1A	*C. album*	32.00	416.23	6	85	0.00
	P. persicaria	13.08	225.11	1	53	0.00
	S. media	7.75	98.25	0	43	0.19
	Total weeds	52.83	743.80	13	118	0.00
KP500P1B	*C. album*	31.40	516.13	9	95	0.00
	P. persicaria	13.80	329.87	1	93	0.00
	S. media	11.66	193.41	0	59	0.17
	Total weeds	56.86	884.36	11	117	0.00
KP500P2A	*C. album*	35.31	438.16	9	96	0.00
	P. persicaria	12.61	119.62	0	33	0.06
	S.vulgaris	0.42	0.99	0	5	0.78
	S. media	33.36	5059.21	0	430	0.03
	Total weeds	81.69	5497.76	24	469	0.00
KP500P2B	*C. album*	27.31	297.63	4	84	0.00
	P. persicaria	11.06	116.11	0	51	0.03
	S. vulgaris	0.09	0.14	0	2	0.94
	S. media	29.29	2124.39	1	211	0.00
	Total weeds	67.74	2736.02	17	237	0.00
KPG216	*C. album*	3.06	13.90	0	16	0.33
	C. bursa-pastoris	4.05	77.06	0	54	0.34
	P. annua	2.91	8.56	0	15	0.19
	P. aviculare	0.09	0.12	0	2	0.92
	P. persicaria	3.45	16.51	0	25	0.22
	S. media	0.31	0.50	0	3	0.80
	Total weeds	13.88	132.68	2	58	0.00
PAV3058	*C. bursa-pastoris*	0.37	0.83	0	5	0.79
	Matricaria spp.	0.09	0.20	0	3	0.96
	S. nigrum	4.82	17.79	0	21	0.16
	Sonchus spp.	0.22	0.23	0	2	0.81
	S. media	0.63	1.04	0	4	0.66
	Total weeds	6.13	20.33	0	21	0.06
PAGV4151AF	*C. album*	2.81	11.63	0	11	0.44
	E. crus-galli	35.75	2713.67	0	170	0.19
	P. annua	8.06	226.20	0	60	0.38
	P. convolvulus	0.44	2.26	0	6	0.88
	P. persicaria	2.50	13.73	0	11	0.50
	S. nigrum	77.06	7020.46	0	210	0.31
	Total weeds	126.63	17308.78	0	361	0.06
PAGV4151BC	*C. album*	0.94	2.46	0	6	0.56
	E. crus-galli	20.50	1246.80	0	128	0.25
	P. annua	3.13	10.25	0	10	0.38
	P. persicaria	1.44	6.26	0	9.00	0.56
	S. nigrum	18.31	405.56	2	85	0.00
	Total weeds	44.31	1902.50	6	137	0.00
PAGV4151DE	*C. album*	2.81	13.36	0	12	0.44
	E. crus-galli	78.19	10194.03	0	320	0.06
	P. annua	10.63	123.85	0	40	0.25

Data set	Weed species	mean	variance	min.	max.	*P*(0)observed
PAGV4151DE	*P. convolvulus*	0.63	2.38	0	6	0.75
	P. persicaria	2.00	9.60	0	10	0.50
	S. nigrum	112.00	2089.47	37	185	0.00
	Total weeds	206.25	9891.13	85	399	0.00
PAGV4152AF	*C. album*	24.75	111.00	6	39	0.00
	P. annua	14.63	132.38	3	38	0.00
	S. media	10.88	153.45	1	47	0.00
	Total weeds	50.25	372.73	25	78	0.00
PAGV4152BC	*C. album*	4.56	17.33	0	12	0.06
	P. annua	1.56	14.00	0	15	0.63
	Total weeds	6.13	44.78	0	23	0.06
PAGV4152DE	*C. album*	19.88	212.38	4	56	0.00
	P.annua	13.06	239.80	0	40	0.38
	S. media	1.31	4.76	0	6	0.63
	Total weeds	34.25	816.20	4	86	0.00
REG3109	*C. bursa-pastoris*	0.85	3.91	0	11	0.71
	C. album	10.15	54.72	1	26	0.00
	E. crus-galli	1.58	7.01	0	15	0.44
	P. annua	38.08	849.01	11	154	0.00
	P. persicaria	0.92	1.65	0	5	0.54
	S. nigrum	34.77	408.90	5	89	0.00
	S. media	15.50	71.83	3	37	0.00
	Total weeds	101.85	957.66	40	200	0.00
VP1008	*C. bursa-pastoris*	0.04	0.06	0	2	0.97
	C. album	0.43	0.94	0	6	0.74
	E. crus-galli	3.52	24.17	0	26	0.28
	P. annua	13.43	148.00	0	65	0.10
	P. aviculare	0.58	1.61	0	8	0.73
	P. convolvulus	0.13	0.35	0	4	0.95
	P. persicaria	9.69	148.42	0	63	0.14
	S. vulgaris	0.02	0.02	0	1	0.98
	S. nigrum	0.58	1.54	0	8	0.69
	S. media	41.11	947.93	4	195	0.00
	Total weeds	69.51	1481.45	18	269	0.00
VP1023A	*C. album*	4.11	26.84	0	24	0.24
	P. annua	15.95	293.97	0	69	0.15
	S. media	14.54	217.44	0	75	0.08
	Total weeds	34.60	752.47	2	143	0.00
VP1023B	*C. album*	1.23	4.00	0	9	0.59
	P. annua	25.59	227.33	3	68	0.00
	S. media	5.38	12.97	0	17	0.04
	Total weeds	32.19	257.77	8	81	0.00
ZW2369	*C. album*	0.35	0.44	0	3	0.73
	P. persicaria	2.73	3.33	0	8	0.15
	P. convolvulus	0.03	0.03	0	1	0.98
	Matricaria spp.	0.18	0.35	0	3	0.90
	Total weeds	3.28	3.03	0	8	0.05

Appendix 2

Species specific values of parameters b *and* $^{10}\log(a)$ for the model $^{10}\log(\text{variance}) = b \times {}^{10}\log(\text{mean}) + {}^{10}\log(a)$, their s.e. and significances ($P < 0.05$).

Weed species	sign for b (0.05)	b	s.e.	sign for a (0.05)	$^{10}\log(a)$	s.e.
E. crus-galli	ab	1.95	0.09	abcdefghi	0.37	0.07
S. media	ab	1.67	0.13	e ghi	0.19	0.12
P. aviculare	abc e	1.67	0.15	abcd	0.78	0.12
P. annua	abc e	1.59	0.12	b efghi	0.32	0.10
P. convolvulus	abcdef	1.50	0.11	abcdefghi	0.85	0.11
C. album	bcde	1.40	0.03	abcd i	0.60	0.04
S. nigrum	bcde	1.39	0.07	bcdefgh	0.49	0.08
C. bursa-pastoris	bcde	1.36	0.13	abcd fgh	0.53	0.09
P. persicaria	bcde	1.36	0.07	abcd f h	0.57	0.07
C. rubrum	abcdef	1.34	0.14	b efghi	0.29	0.08
Sonchus spp.	abcdef	1.29	0.15	b defghi	0.32	0.07
S. vulgaris	cdef	1.24	0.03	abcdefghi	0.43	0.05
Matricaria spp.	bcdef	1.18	0.15	abcdefghi	0.37	0.12
S. tuberosum	def	0.78	0.20	efghi	0.19	0.12