

Timing of disturbance and vegetation development: how sowing date affects the weed flora in spring-sown crops

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Abstract. The number of annual weeds were recorded in 752 field experiments in spring-sown cereal crops conducted in Sweden 1972-1993. Two null hypotheses were tested regarding how the sowing date influenced the weed flora. 1. There is no relationship between the weed flora composition and sowing date. A pCCA (with geographic regions, crop species and soil types as covariables) clearly refuted this hypothesis. Hence, the composition of the weed flora varied depending on sowing date. 2. Species classified as summer annuals, winter annuals and germination generalists (that can germinate substantially in both spring and autumn) do not differ in their placement along the first ordination axis in the pCCA, i.e. according to sowing date. An ANOVA was unable to reject this hypothesis. Hence, germination syndrome classification did not explain the observed community differences related to sowing date. These results illustrate the importance of the date of disturbance for any secondary succession involving a seed bank and also the importance of annual dormancy cycles in seed banks.

Keywords: Community; Partial CCA; Summer annual; Sweden; Variation partitioning; Winter annual.

Nomenclature: Tutin et al. (1964-1980).

Abbreviation: pCCA = Partial Canonical Correspondence Analysis.

Introduction

The timing of disturbance will affect which seeds are available for germination and determine conditions for germination and subsequent growth (Busing & Clebsch 1983; Squiers 1989). For example, germination is determined by temperature and moisture availability that can vary seasonally. Seed availability is determined not only by the presence of seeds but also by their dormancy status, which may vary with season. It is well known that the flora in spring- and autumn-sown crops in temperate climates differ substantially (Andersson & Milberg 1998; Hallgren et al. 1999; Hald 1999). Another example of temporal shifts in species composition is the successive

communities of summer annual and winter annual species in the Chihuahuan Desert (Gou & Brown 1996).

The periodicity of seedling emergence within a season, recorded in detail mainly in annual weed species, differs between species (Lauer 1954; Roberts & Feast 1970; Stoller & Wax 1973; Erviö 1981; Håkansson 1983; Ogg & Dawson 1984; Roberts 1984; Bond & Baker 1990; Egley & Williams 1991; Popay et al. 1995; Kotorova & Lepš 1999). Therefore, there is reason to believe that the actual timing of a disturbance within the spring or autumn could affect the composition of the developing vegetation, as suggested in previous reports on Swedish weed communities (Andersson & Milberg 1996; Hallgren et al. 1999; Milberg et al. 2000).

In this study we test hypotheses regarding the importance of the sowing date of spring-sown crops on the composition of the weed community. We used data on number of weed plants in unsprayed control plots in 752 field experiments conducted over a 22-yr period in spring-sown cereal crops in Sweden. The first null hypothesis tested was that:

(1) *there is no relationship between the weed flora composition and sowing date after covarying out the influence of geographic location, soil type, and crop* (tested with a Monte Carlo permutation test on the first ordination axis in a pCCA). If refuted, we wanted to explore patterns further by testing another null hypothesis:

(2) *species classified as summer annuals, winter annuals and germination generalists (that can germinate substantially in both spring and autumn) do not differ in their placement along the first ordination axis in the pCCA, i.e. according to sowing date.* We tested this with ANOVA of ordination scores. We had explicitly stated these null hypotheses before the onset of data analysis (cf. Hallgren et al. 1999). Finally, to evaluate the amount of variation uniquely described by sowing date relative to four other groups of variables (crop species, geographic region, soil type, year) and jointly described by sowing date and these variables, we partitioned the explainable variation between them (Økland & Eilertsen 1994; Økland 1999).

Methods

Data on the number of individuals of annual weed species were collated from unsprayed control plots from 752 annual, on-farm field experiments conducted between 1972 and 1993 to evaluate new herbicides against dicotyledonous weeds. The experiments were carried out in spring-sown cereal crops in the southern half of Sweden. Sowing dates ranged from March 9 to June 7 (median: May 4). Seedlings that have emerged before the sowing date are normally killed during seed bed preparation and the sowing operation.

Each experiment consisted of four blocks with randomly distributed plots within the blocks. In late June or early July, the number of annual weed plants per species were counted in at least two sample plots (each of 0.25 m²) per treatment plot. According to the sampling protocol for the experiments, the sample area should be sufficiently large to include at least 20 plants of the most frequent species within untreated plots. Occurrence of a species in an experiment was only noted when there were ≥ 5 individuals per m². Species with fewer individuals were grouped together in an ‘other weeds’ category.

In the present analysis, we used data on the 20 most abundant annual species and species groups (Table 1) and excluded experiments from northern Sweden, where few experiments had been conducted, the weed flora is species-poor and where the sowing date is often much later than in the south of Sweden.

When evaluating the relationship between sowing date and the weed community, we classified the species as ‘summer annuals’, ‘winter annuals’ or ‘germination generalists’ being able to germinate substantially in both autumn and spring (Table 1). From a germination ecology perspective the two latter would be considered facultative winter annuals (Baskin & Baskin 1998) and the distinction between them is subjective. The classification (Table 1) is according to Swedish conditions and is based on literature (Fogelfors 1977; Håkansson 1995) and our previous field experience of the species.

We performed partial Canonical Correspondence Analysis (pCCA; ter Braak 1988) treating sowing date as an ‘environmental variable’. Previous studies, using a parallel data set on weed biomass, had shown that the weed community varies geographically and with soil type (Hallgren et al. 1999) and there is reason to believe that the crop species itself may influence the weed community (Erviö & Salonen 1987; Andersson & Milberg 1998). Therefore, we treated the following as covariables: ‘crop species’ (wheat, rye, oats), ‘soil type’ (seven types: sandy soil; fine sand soil; silty soil; loamy soil; silty clay loam; heavy to very heavy clay soil; organogenic soil) and ‘geographic region’ (seven regions: Skåne & Hallands län; Blekinge, Gotland & Kalmar

Table 1. Weed taxa recorded, their frequency in the 752 experiments and their ranking in a pCCA with ‘sowing date’ as the only environmental variable (‘geographic region’, ‘crop species’ and ‘soil type’ were included as covariables). High numbers indicate affiliation with experiments sown early and negative ones with late sowing dates.

Species	Frequency (%)	Sowing date ranking
Summer annuals		
<i>Polygonum aviculare</i>	5.3	0.2502
<i>Sinapis arvensis</i>	3.9	0.2443
<i>Fumaria officinalis</i>	13.8	0.1665
<i>Bilderdykia convolvulus</i>	17.0	0.1644
<i>Polygonum lapathifolium/persicaria</i>	12.4	0.0947
<i>Chenopodium album/suecicum</i>	43.6	0.0006
<i>Galeopsis bifida/speciosa/tetrahit</i>	33.6	-0.0638
<i>Sonchus asper/oleraceus</i>	2.5	-0.0614
<i>Erysimum cheiranthoides</i>	6.1	-0.3098
<i>Spergula arvensis</i>	8.6	-0.3741
Winter annuals		
<i>Myosotis arvensis</i>	15.6	0.0939
<i>Veronica agrestis/arvensis/hederifolia/persica</i>	3.3	0.0648
<i>Galium aparine/spurium</i>	12.4	0.0001
<i>Matricaria perforata</i>	10.9	-0.0360
<i>Capsella bursa-pastoris</i>	5.1	-0.2430
Germination generalists		
<i>Lamium amplexicaule/hybridum/purpureum</i>	15.6	0.2004
<i>Thlaspi arvense</i>	7.0	0.0264
<i>Stellaria media</i>	36.3	-0.0093
<i>Viola arvensis</i>	27.9	-0.0281
<i>Lapsana communis</i>	7.2	-0.0824

län; Jönköpings & Kronobergs län; Västra Götalands län; Östergötlands län; Uppsala, Stockholms, Södermanlands, Västmanlands & Örebro län; Kopparbergs, Gävleborgs & Värmlands län). Each group of variables was entered as a number of dummy variables in the analysis. We employed the default options in CANOCO 4 (ter Braak & Šmilauer 1998), except that we square-root transformed weed numbers. We tested the significance of ‘sowing date’ using a Monte Carlo permutation test (2000 permutations) of the first ordination axis in the pCCA, with permutation blocks defined by the categorical covariables (ter Braak & Šmilauer 1998).

We employed variation partitioning to quantify the unique contribution of each variable or group of variables (if categorical) in explaining species composition (e.g. Økland & Eilertsen 1994; Roche et al. 1998). Økland (1999) argued that the total inertia was an inadequate measure of the total variation in a data set. We therefore followed his recommendation and partitioned only the variation explained by our variables. Apart from the covariables used in the pCCA above, we also included ‘year’ as a group of categorical covariables in the variation partitioning. The purpose was to quantify the possible overlap in explanatory power between ‘year’ and ‘sowing date’.

Results

Relationship between weed flora and sowing date

The eigenvalue of the first ordination axis, i.e. the sowing date axis, was low (0.0157), which is not surprising since the effects of ‘geographic region’, ‘soil type’ and ‘crop species’ had been covaried out. More importantly, the sowing date significantly influenced the weed flora recorded later in the season (Monte Carlo test: F -ratio = 2.234; P -value = 0.0035). Hence, the first null hypothesis was refuted.

Germination syndromes and species scores along the first ordination axis

Summer annuals, winter annuals and germination generalists did not differ significantly in their scores on the first ordination axis, i.e. the sowing date axis (ANOVA, $F_{(2,17)} = 0.09262$, $P = 0.9120$). Instead, there was a substantial variation in ordination scores within each group (Table 1). Hence, the second null hypothesis could not be refuted.

Variation partitioning

The partitioning of the explainable variation in the data set revealed two things. First, comparing the groups of variables, it is clear that ‘sowing date’ and ‘crop species’ are much less important for explaining variation in the weed community than ‘geographic region’, ‘soil type’ and ‘year’ (Table 2). Second, comparing the intersection of ‘sowing date’ and each of the other groups of variables revealed that ‘sowing date’ explained unique variation compared to ‘year’ and ‘soil type’, but that the influence of ‘sowing date’ to some degree depended on ‘geographic region’ (Table 2).

Discussion

Relationship between weed flora and sowing date

There was a clear and significant effect of the sowing date on the weed flora recorded later in the season. Hence, the weed species composition varies depending on when sowing is conducted within a relatively short time period in the spring. It is slightly surprising that such a clear and interpretable pattern could emerge from data from such a large geographic area and collected by numerous people over many years. It is possible that the value of large survey data sets is underestimated when it comes to strict hypothesis testing of the type conducted here (cf. Hallgren et al. 1999). Nevertheless, a word of

Table 2. Partitioning of the explainable variation among the five groups of variables. $T|U$ is the variation described by T but not explained by U . $T \cap U$ is the variation jointly described by T and U . $U|T$ is the variation described by U but not by T . Values are percentage of total variance explained by T and U .

T	U	Percentage of explainable variation		
		$T U$	$T \cap U$	$U T$
Sowing date (D)	CSGY	2.0	4.0	94.0
Crop (C)	DSGY	1.6	2.4	96.0
Soil type (S)	DCGY	21.3	13.3	65.4
Geographic region (G)	DCSY	26.2	16.8	57.0
Year (Y)	DCSG	30.6	2.1	67.4
D	C	55.0	10.0	35.0
D	S	13.5	1.7	84.8
D	G	4.8	8.7	86.5
D	Y	15.2	0.6	84.2

caution is appropriate. First, there might be confounding factors that were not considered (e.g. local weather variation that independently might affect the farmer’s choice to sow and weed germination). Second, the variables chosen might not describe the variation to the extent expected (e.g., our soil and geographical variables do not factor out all soil and geographic variation).

The reason for the documented temporal shift in species composition could be attributed to different temperature requirements for germination among species, since temperature increases more or less steadily during the spring in Sweden (Milberg 1994a; Milberg & Andersson 1997) while moisture does not become limiting for germination until late in the spring and only in some years. We believe, however, that the seasonal changes in germinability, described in many annual species from temperate areas (Baskin & Baskin 1985), in combination with rising soil temperatures cause for the shift in species composition. For example, typical summer annuals have seeds that are germinable in the spring but dormant in the autumn. The low temperatures during winter reduce the seed dormancy level, while high temperatures strengthen dormancy. Winter annuals, on the other hand, respond differently to temperature, causing low dormancy in autumn and often a strengthening of the seed dormancy during the winter (Baskin & Baskin 1998). Although these behaviours are best described in annual weed species (Håkansson 1983, 1992; Bouwmeester & Karssen 1993a,b; Milberg & Andersson 1997; Baskin & Baskin 1998) they are also present in species from other types of habitat as well as in perennial species (Baskin & Baskin 1990, 1994; Baskin et al. 1993a,b, 1996, 1999a,b; Milberg 1994a-c; Schütz 1997, 1998). Therefore, we believe that similar temporal shifts in the community emerging after a disturbance can be expected in any type of community where seasonal dormancy cycles prevail.

The species with extreme pCCA ranking (i.e. < -0.15 and > 0.15 in Table 1) would, according to our explanatory model, have dormancy patterns and seasonal seedling emergence patterns with clear peaks early or late in the spring. For example *Polygonum aviculare*, *Sinapis arvensis*, *Lamium* spp., *Fumaria officinalis* and *Bilderdykia convolvulus* should peak early while *Capsella bursa-pastoris*, *Erysimum cheiranthoides* and *Spergula arvensis* would peak late. Such a prediction could be tested by correlating the species scores presented here with those from an experiment where, e.g. seeds of these species have been sown together. Although there is, as yet, no such comparative data set available, the prediction can partly be tested with the aid of published records from Sweden and the UK. Håkansson (1983), reporting temporal emergence patterns for three of these species (12 in total), confirmed the late emergence of *Capsella bursa-pastoris* and early emergence of *Bilderdykia convolvulus*. *Spergula arvensis*, however, had a relatively even emergence throughout the spring (Håkansson 1983). Milberg & Andersson (1997) studied dormancy cycles in two of these (8 species in total) and noted a minimal dormancy level in June and August in *Spergula arvensis* and *Capsella bursa-pastoris*, respectively. Records from the UK might be less relevant because of climatic differences, as well as potential genotypic ones in the weed populations. Nevertheless, *Polygonum aviculare*, *Fumaria officinalis* and *Bilderdykia convolvulus* had clearer and earlier peaks than *Spergula arvensis* and *Capsella bursa-pastoris* in a comparative study (Roberts & Feast 1970).

It is worth pointing out that dormancy cycles also have implications for the methodology used when studying soil seed banks by allowing seeds to germinate and count seedlings. I.e., the composition and amount of seedlings emerging from soil samples will depend on timing of soil sampling (Milberg & Andersson 1998) and on possible pre-treatments of the samples (e.g. Milberg 1995).

Germination syndromes and sowing date

The pCCA ranking of species according to sowing date was not significantly different between summer annuals, winter annuals and germination generalists. Instead, there was a surprising differentiation between summer annuals that germinate early and late (Table 1, see also discussion above). Among the winter annuals and germination generalists only *Capsella bursa-pastoris* and *Lamium* spp., respectively, had extreme rankings in the pCCA (late vs. early sowing). In conclusion, the germination syndrome was not very helpful in describing differences in temporal patterns of seedling emergence in the spring. Nevertheless, it must be pointed out

that it is not only the time of sowing that varies, but also soil moisture and temperature. Hence, seedling emergence and growth might be delayed after early sowing because of low soil temperatures, and also after late sowing in the absence of rainfall. Furthermore, the classification according to the germination syndrome does not fully reflect the complexities of these life-history types, nor is the classification definite in all cases (e.g. Bouwmeester & Karssen 1993c).

One aspect complicating the interpretation, and possibly obscuring the patterns in the data, is that the exact pattern of the dormancy cycles (both periods with minimal dormancy and the temporal extent of the non-dormancy period), might vary between years. Since the gross dormancy patterns are determined by temperature regimes (at least in humid, temperate areas) (Baskin & Baskin 1998) and not by Julian day numbers, such differences could be expected and have, in fact, been noted in several cases where seedling emergence has been recorded over several years (Roberts & Potter 1980; Roberts & Boddrell 1983; Ogg & Dawson 1984; Egley & Williams 1991; Popay et al. 1995; Buhler 1997). Nevertheless, the variation partitioning suggested that such interannual variation is relatively small, since the intersection between 'sowing date' and 'year' was small (Table 2).

Variation partitioning

We employed variation partitioning mainly to find out to what extent 'sowing date' explained unique variation relative to a number of other variables. More specifically, we had expected 'sowing date' to vary with soil type (e.g. later sowing on organogenic soils) and between geographic regions (earlier sowing in the south) and hence that there would be only a small fraction of unique variation explainable by 'sowing date'. Our expectations were partly fulfilled, since the intersection term between 'sowing date' and 'geographic region' was relatively large (Table 2). Hence, the earlier sowing in southern Sweden could partly explain the different weed community composition of this region (Hallgren et al. 1999; note that this effect had been covaried out in the pCCA, so that the ranking of species in Table 1 was conservative). The explanatory power of 'soil type', however, did not overlap much with 'sowing date' (Table 2).

It is not surprising that 'soil type', 'geographic region' and 'year' emerged as the three most important groups of variables. They consist of several categorical variables each (explained variation is, in part, a function of the number of variables), and each of them is known to be of major (Hallgren et al. 1999) or intermediate (Milberg et al. 2000) importance in a parallel data set on weed biomass. Although the magnitude of the influence

of 'sowing date' might appear modest compared with the other variables, it was large enough to provide significant pattern and explain more of the variation than the crop species could (Table 2).

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