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Management practices influence the competitive potential of weed communities and their value to biodiversity in South African vineyards

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Summary

Weeds have negative impacts on crop production but also play a role in sustaining biodiversity in agricultural landscapes. This trade-off raises the question of whether it is possible to promote weed communities with low competitive potential but high value to biodiversity. Here we explored how weed communities respond to different vineyard management practices in South Africa's Western Cape, aiming to identify whether any specific practices are associated with more beneficial weed communities. Eight weed community characteristics representative of abundance, diversity and functional composition were used as indicators of competitive potential and biodiversity value. We explored how these responded to farm management strategy (organic, low input or conventional) and weed management practices (herbicides, tillage, mowing, or combinations of these) using ordination and mixed models. Mown sites were associated with weed communities of high biodiversity value, with higher weed cover in both winter and summer, higher diversity and more native weeds. Mowing also promoted shorter weeds than either tillage or herbicides, considered to be less competitive with grapevines. However, high summer weed cover may be problematic where competition for water is critical, in which case tillage offers a method to limit summer weed cover that did not adversely affect diversity or native weeds. In contrast, herbicide-treated sites had characteristics indicative of a lower biodiversity value and higher potential for competitiveness with few native weeds, lower diversity and relatively tall, small-seeded weeds. Mowing in winter combined with tillage in spring may thus optimise the biodiversity benefits and production costs of Western Cape vineyard weeds.

Keywords: weeds, weed management, plant community, biodiversity, competition, vineyards, organic, functional traits

Introduction

Weeds can negatively impact crop production by competing with crops for resources (Oerke 2006), and consequently substantial effort and resources are invested into weed control to maintain crop yields (Atwood & Paisley-Jones, 2017). However, current weed control strategies appear unsustainable, with intensive tillage and herbicide use associated with environmental risks (Van Oost *et al.,* 2006; Annett *et al.,* 2014) and the spread of herbicide resistance (Mortensen *et al.,* 2012). Furthermore, the reduced abundance and diversity of weeds in farmed landscapes has been linked to declines in species at higher trophic levels, including insects and birds (Marshall *et al.,* 2003).

This trade-off between the negative impacts of weeds on crop production and the negative impacts of weed control on the environment has prompted researchers to question whether it is possible to select for weed species that are minimally competitive with crops but that support high levels of biodiversity (Storkey & Westbury, 2007; Mézière *et al.,* 2015). If a weed community is composed of less competitive species, then weed control actions could be reduced and more weeds conserved for biodiversity purposes at less cost to crop production. Likewise, if the weed numbers are limited by crop production requirements, then for environmental purposes it would be preferable if the weeds retained were of higher value to biodiversity.

Plant 'response-effect' functional traits provide a framework to investigate how agroecosystem conditions can determine the types of weeds present, and also to understand what effects the weeds will have on the agroecosystem (Lavorel & Garnier, 2002). Farm management actions, as well as local environmental conditions, select for or against specific traits and thus determine which species of weeds can survive in a given agroecosystem (Navas, 2012). For example, agricultural intensification is characterised by increased resource availability and an increased frequency and/or intensity of disturbance experienced by weeds. These conditions select for traits that allow weeds to exploit available resources to maximise growth and reproductive output in a short timeframe between disturbances (Gaba *et al.,* 2014; Garnier & Navas, 2012). However, such species may be particularly competitive with crops, given that rapid growth is associated with rapid resource acquisition (Reich, 2014), which could lead to rapid sequestering of resources by weeds away from crops.

Farm management can also affect weed diversity by filtering out species that do not have the requisite traits for survival, and this can influence the effect of the weed community on the surrounding agroecosystem. Species diversity can enhance the diversity, magnitude and resilience of ecosystem functions provided by a community (Díaz & Cabido, 2001). In particular, increased weed community diversity is known to increase support for biodiversity at other trophic levels (Bárberi *et al.,* 2010). Management actions that impose high selection pressure for specific traits, such as herbicides and tillage, tend to reduce diversity to a greater degree than actions that impose lower selection pressure (Gaba *et al.,* 2014).

Knowledge of both the diversity and functional composition of a weed community is thus required to understand whether it is possible to promote a weed community that has relatively high biodiversity value, yet relatively low competitive potential. In this study, we explored how these characteristics of weed communities were influenced by management actions in vineyards of South Africa's Western Cape. Managing weeds to promote biodiversity may assist conservation in a region known for its unique assemblage of native species (Gaigher & Samways, 2010). However, the Western Cape has a semi-arid climate and water availability in the dry summer is critical for grape production. It is thus important to balance the biodiversity benefits of weeds with their potential to compete with grapevines.

Previous studies of vineyard weeds indicate that management practices do affect weed communities in terms of composition, diversity (e.g. Lososová *et al.,* 2002, Gago *et al.,* 2007) and abundance of individual species (e.g. Ferrara *et al.,* 2015). Weed diversity typically decreases as either soil disturbance or herbicide use increase, indicating that these have a stronger filtering effect on weeds than alternative floor (soil and vegetation) management practices such as mowing (Bruggisser *et al.,* 2010, Sanguankeo & León 2011, Kazakou *et al.,* 2016). Kazakou *et al.,* (2016) used the response-effect trait framework to explore how management filters that select for different weed species may influence the impact of weeds on grape production. Their study identified that tillage compared with mowing reduced both weed diversity and weed biomass and also promoted species with traits associated with faster growth. However, they observed no significant difference in vine water stress or grape yield between treatments.

In this study, we assessed whether weed communities found under different management practices in Western Cape vineyards differed in their competitive potential and biodiversity value. We first surveyed the weed flora in vineyards employing a range of management practices and used multivariate analyses to explore how weed community composition varied in relation to both management and pedoclimatic conditions. Secondly, we used eight weed community characteristics based on weed abundance, diversity and functional composition as indicators of biodiversity value or competitive potential in the context of Western Cape vineyards (indicators and their justification are described in *Materials and Methods*). Regression models were used to investigate whether variation in these community characteristics was linked to different management practices. In accordance with the literature discussed above, we hypothesised that management practices imposing a stronger filter on weeds (herbicides and tillage) would reduce weed diversity. Strong filters were also expected to select for specific functional types of weeds (those possessing the requisite traits to survive the filters). We aimed to identify whether any specific management filters were associated with community characteristics that increased the value to biodiversity of the weed community whilst decreasing its competitive potential with grapevines.

Methods and materials

Study location and timing

Weed composition, community characteristics, management practices and selected environmental variables were surveyed in 14 vineyards in the Stellenbosch wine region of South Africa's Western Cape. Vineyards were located between latitudes -33°12' and -33°14', longitudes 18°47' and 19°15', and elevations of 60 m a.s.l to 430 m a.s.l. Climatic conditions within the study area are influenced by local topography, with average annual temperatures ranging from 15.5°C to 18.2°C and mean annual rainfall ranging from 554mm to 1087mm (Schulze 1997).

Weed surveys took place over seven weeks between 18 July 2016 and 31 August 2016 to avoid significant changes in composition from early-season to late-season weed species (Hanzlik & Gerowitt, 2015). Vineyards were surveyed at least eight weeks after the most recent weed management event, to allow any weeds that were going to re-establish following the control effort to do so. A second follow-up survey was also conducted between 1 December 2016 and 15 December 2016 to assess summer weed cover.

Sampling design

Selection of vineyards with a range of management practices - To maximise the variation in management practices included in this study whilst minimising environmental variation, we first arranged permission to conduct the study on four organic vineyards. A further two or three non-organic vineyards near each of the organic vineyards were then selected based on whether the vineyard managers could be contacted, to bring the total number of vineyards in the study to 14. At the time of the study, three of the organic vineyards were certified to European Union organic standards and thus had been under organic management for at least two years. One vineyard was in the two-year conversion period to these standards, but had been mostly chemical-free for the last six years and was considered organic for the purposes of this study.

Within each vineyard, surveys were conducted in two separate ‘blocks’ of vines: a block is a stand of vines of the same cultivar within which vine and floor management is consistent (the equivalent of a ‘field’ in arable crop and pasture studies). Blocks varied in size between vineyards, with smaller blocks approximately 100 m long x 50 m wide and larger blocks around 250 m x 250 m. Following data collection, it was decided to exclude three blocks (each from a different vineyard) from further analysis due to substantial changes in weed management within the past year: persistence in the seedbank of weeds adapted to the previous management regime may have obscured the relationship between management and community composition.

Survey layout within each vineyard - In each block, weeds were surveyed in four split quadrats, with one half of each quadrat over the vine row and the other half in the inter-row (Fig. 1c). Each half of the split quadrat was 1m x 6m (the whole quadrat was 2m x 6m). Management often differs between the row and inter-row as most farmers prioritise weed control within the vine rows (see Supporting Information Appendix S1). This design meant that soil samples (see below: *Weed community composition and characteristics*) taken from the midline of the split quadrat could be used to represent the whole quadrat, minimising soil testing costs to maximise the number of vineyards surveyed. To account for possible variation in the weed community between the edges and centres of vineyard blocks (José-María *et al.,* 2010), two quadrats were placed on block edges at opposite corners of each block and two quadrats were placed randomly within the central area of the block, at least 20m away from the nearest block edge.

Fig. 1 near here

Weed community composition and characteristics

Weed community composition was sampled by visually estimating the percent cover of each species in each quadrat using the Domin scale, a ten-point cover scale with higher resolution at low cover scores to capture variation in rare species (Table 1). The scale is preferable to plant density as a measure of abundance given the difficulties of distinguishing individual plants in mat-forming grasses and similar species (Kent, 2012). For analysis, the Domin scores (see Table 1) were converted to numerical scores by taking the mid-point of each Domin percent cover band (Lepš & Hadincová, 1992).

Table 1 near here

Eight community characteristics representing the potential competitiveness or potential biodiversity benefits of weeds were selected (Table 2). The first four related to the potential of the weed community to support biodiversity of other trophic levels: weed species richness, species diversity, ground cover by weeds in winter and ground cover by native weeds. Together, these four characteristics are expected to increase with the value of the weed community to biodiversity at other trophic levels, through increasing the diversity and abundance of resources provided (Bárberi *et al.,* 2010; Sanguankeo & León, 2011) and to specifically increase support for native biodiversity, which may have a weaker relationship with introduced plant species (McCary *et al.,* 2016). The fifth community characteristic was weed cover in summer, which would provide further resources to biodiversity, but is also considered by local farmers as more likely to impact grapevine growth due to competition for limited soil moisture in summer. Winter weed cover, native weed cover and summer weed cover were assessed for each quadrat using visual estimates following the Domin scale (see above in *Survey layout within each vineyard*; winter weed cover was assessed between July and September and summer weed cover during an additional follow-up survey in December). For species diversity, the Shannon diversity index for each quadrat was calculated based on the Domin cover midpoints of each species observed.

Table 2 near here

The final three community characteristics were the community-weighted means (CWM) of three functional traits considered key indicators of a plants' life history strategy: seed mass, specific leaf area (SLA) and height (Garnier & Navas 2012). These traits indicate whether species have a 'fast' (ruderal) or 'slow' (tolerant of stress and competition) resource economic strategy (Grime, 1977; Westoby, 1998; Reich, 2014). 'Fast' species (tall, high SLA, small seeds) exploit readily available resources to invest in rapid biomass production to capture resources faster than their neighbours, while 'slow' species (short, low SLA, large seeds) invest in resource conservation and stress tolerance mechanisms and can thus perform well at lower resource availabilities. In general, 'fast' traits would be expected to increase competition with crops, given that agroecosystems are typically resource-rich environments. For example, vineyards do not have a closed canopy cover (high light availability), and are often irrigated (high water availability) and fertilised (high nutrient availability). Consequently, we would expect weed communities with higher CWMs for SLA and height and a lower CWM for seed mass, to be more competitive with grapevines. Height in particular is expected to confer competitiveness with grapevines. Height is linked to rooting depth and therefore tall weeds are expected to overlap more with grapevines in the soil layers from which they seek water (Garnier & Navas 2012) and thus impose greater competitive pressure. Furthermore, local vineyard farmers mentioned tall weeds as being difficult to control and more likely to interfere with vine management, due to their tendency to grow into the vine canopy.

To calculate the CWMs for the trait-based community characteristics, the trait value of each species was multiplied by the proportion of each species in each quadrat and these weighted values then summed to give the overall CWM for each quadrat. Trait values for each species were acquired from the TRY Global Traits Database (Kattge *et al.,* 2014). The identification codes (TraitID) for the traits used were 11: SLA, 18: plant height and 26: seed dry mass. A single trait value for each species estimated by taking the mean of all standard values for all ‘mean’, ‘median’, ‘best estimate’ and ‘single’ entries in the open access section of the database. The TRY database was chosen over other databases due to its global remit (most other databases are confined to observations from either Europe or North America), given that no locally collected trait data were available. Acquiring trait means from a global database may not equate to accurate trait means for weed populations in South Africa, nor take into account intraspecific trait variation, but is sufficient for the purpose of obtaining a broad idea of how trait values vary between weed communities under different management practices. The TRY database did not contain records for all traits for all species observed in this study, so to account for these missing values, quadrats were only included in the analyses for each trait if at least 75% of their weed cover comprised species for which trait values were available. This ensured the CWMs for each quadrat were representative of the majority of species present. For the analyses including height, 172 quadrats were used (86% of the total sample); for SLA, 145 quadrats (73%); and for seed mass, 134 quadrats (67%).

To summarise the eight community characteristics, a weed community that is considered to maximise value to biodiversity whilst minimising potential for competition would be more diverse, contain more native species, would cover more ground in winter but less in summer, and would be composed of shorter species with larger seeds and a lower SLA (Table 2).

Management categories and environmental variables

Measures of environmental variables known to be important to weed community composition (Hanzlik & Gerowitt, 2015) were collected from each quadrat according to the methods in Table 3, on the same date as the winter weed survey of each vineyard. Also on that date, information on management practices employed in each block of each vineyard was acquired by asking vineyard managers to fill out a questionnaire on what activities they undertook to manage weeds. A wide range of weed management practices were reported, all of which varied in type, frequency and timing between vineyards, and different vineyards applied different techniques to rows and interrows (see results summarised in Supporting Information Appendix S1). To simplify this variation, each quadrat was assigned to a management type category based on the three most common practices (herbicides, tillage and mowing), or combinations thereof (Table 4). Tillage is here defined as any disturbance or overturning of at least the top 2cm of soil; the range of tillage techniques employed by vineyards in this study included harrowing, disc plough and hoeing. Sites were also categorised by the management strategy of the farm in which they were located: either organic, low input or conventional (see defining criteria in Table 4). Fertilisation type and quantity correlated strongly with whether a farm was organic, low input or conventional, and we thus consider part of the effect of management strategy to include the effect of fertilisation. We examined the data for any link between irrigation, weed community composition and community characteristics using the analyses described below, but none was found and so this is not further considered. The survey was undertaken during the wet season when irrigation is used minimally and unlikely to have a large impact on soil water availability.

Tables 3 & 4 near here

Data analysis

Community composition: NMDS ordination - To assess variation in weed species composition between vineyard blocks, we employed a non-metric multidimensional scaling (NMDS) ordination based on the Bray-Curtis dissimilarity measure, using the cover scores of each species present in each quadrat. Sufficient dimensions were included in the ordination to reduce stress to below 0.2 (Kent, 2012). Relationships between management and environmental variables and species composition were explored by fitting explanatory variables as vectors to the ordination in the direction of most rapid change of each variable. The strength of the correlation between the vector and the ordination was assessed using the squared correlation coefficient (R^2) and the significance of the correlation tested using random permutations of the data. This approach of using an NMDS with fitted vectors of explanatory variables was selected over constrained ordination approaches due to the large number of explanatory variables and multicollinearity between these. Given these constraints, an NMDS provides a more reliable method to identify which explanatory variables are most strongly related to species composition (Kent, 2012). The analysis was conducted in R (R Core Team, 2017) using the *vegan* package.

Community characteristics: mixed effects linear regression models - To assess relationships between management type and community characteristics, and between environmental variables and community characteristics, generalised linear mixed models were used. To take into account the nested sampling structure of this study, the vineyard, block and quadrat of each sample were included as random effects in the mixed models. Fixed effects included management strategy, management practices, whether or not a site was located at the edge or centre of a vineyard block and key environmental variables. Management strategy was either organic, low-input or conventional (Table 4) and management practices were included as a single variable with six levels: mowing, tillage, herbicides, mowing + tillage, mowing + herbicides and tillage + herbicides. No vineyard used all three in any one quadrat (Supporting Information Appendix S1). Only key environmental variables were included in the models due to collinearity between environmental variables. Those included were identified as representative of the main environmental gradients associated with variation in species composition through fitting vectors to the ordination.

All community characteristics except for native weed cover could either be directly modelled with a linear model based on the Normal distribution, or in the case of the trait CWMs, log-transformed to fit the Normality assumption*.* These linear mixed models were calculated using restricted maximum likelihood (REML) and *P*-values for the fixed effects were calculated using Type 3 F tests based on Satterthwaite's approximations, an appropriate technique for unbalanced linear mixed models (Bolker *et al.*, 2008). Given the limited availability of trait data from TRY and subsequent exclusion of some samples from the tests for some traits, not all models were balanced. For the model of native weed cover, a generalised linear model with Poisson distribution and a log link function was used and *P*-values estimated using a likelihood ratio test (Bolker *et al.,* 2008). Post-hoc pairwise comparisons between management categories were calculated based on estimated marginal means, using a Tukey adjustment. These analyses were undertaken in R, using a combination of *lme4, lmerTest,* and *emmeans* (R Core Team, 2017).

Results

115 weed species were observed across the fourteen vineyards in this study, of which 16 species were native to South Africa's Western Cape (Supporting Information Appendix S2). The most widespread and abundant weeds were *Lolium* spp., considered by local researchers to be a hybrid complex consisting primarily of *Lolium rigidum* Gaudin*,* with contributions from *Lolium multiflorum* Lam. and *Lolium perenne* L*.* A three-dimensional NMDS ordination was selected to represent the variation in weed species composition between quadrats, as three dimensions reduced stress to below the accepted limit of 0.2 whilst maximising interpretability (Fig. 2, stress = 0.19). The ordination indicates that both differences in management practices and in environmental conditions are associated with differences in weed community composition. In particular, the first axis of the ordination represents a shift from organic sites managed primarily by mowing to conventional sites managed with herbicides and the second axis represents a continuum from dry, sandy sites to wet sites with higher clay content in their soils (Fig. 2). Sites treated with herbicides were associated with a higher abundance of *Lolium* spp. and *Helminthotheca echioides* (L.) Holub*,* mown sites with the native *Melinis repens* (Willd.) Zizka, and native *Oxalis pes-caprae* L. and tilled sites with *Erodium moschatum* (L.) L'Hér. and *Raphanus raphanistrum* L. (Fig. 2). Within herbicide-treated (sprayed) sites, *Lolium* spp. were more common in drier sandier areas and *H. echioides* more common in more fertile clay soils. On mown organic sites, *O. pes-caprae* favoured areas with clay soils that received more rain, while *M. repens* was found in drier sandier soils.

Fig. 2 near here

Weed communities under different conditions not only differed in species composition, but also in the eight community characteristics reflective of competitive potential and value to biodiversity. Correlating the community characteristics to the ordination (Fig. 2) indicated that mown organic sites tended to have a higher winter weed cover, a higher native weed cover and a higher CWM for seed mass. In contrast, sprayed sites had a higher CWM for height. Richness and diversity were more strongly related to axis 2, which was associated with environmental variation. Both were higher where rainfall and elevation were higher and soil phosphorous was lower. Summer weed cover was higher where rainfall was higher (Fig. 2).

These trends apparent in the ordination were supported by the regression models. Management practices (mowing, tilling, herbicides and combinations thereof) had a significant ($P<0.05$) association with all community characteristics except for species richness, which was linked to average annual rainfall (Table 5). It was possible to identify pairwise differences between management practices for winter weed cover, summer weed cover, native weed cover and the seed mass CWM (Fig. 3); mowing tended to promote higher weed cover in both winter and summer and a higher cover by native weeds. Tillage was linked to the lowest summer weed cover and weeds with larger seeds. There was also a trend toward taller weeds in tilled and sprayed quadrats compared with mown quadrats, and toward lower SLA CWM in sprayed quadrats. Shannon diversity appeared to be higher in quadrats not treated with herbicides (Fig. 3, Table 5).

Fig. 3, Table 5 near here

In general, community characteristics appeared to respond more strongly to the management practices directly applied to a site than to either the overall management strategy (organic, low input or conventional) or environmental conditions on a vineyard. Management strategy only affected winter weed cover ($P<0.05$, Table 5), with pairwise comparisons (not shown) indicating that organic vineyards had a higher weed cover than conventional vineyards, and low input vineyards were intermediate. There was some evidence ($P<0.1$) that an organic management strategy may also have promoted a higher species richness (Table 5). These two community characteristics were also influenced by environmental conditions; sandier sites had a higher winter weed cover, and sites with higher rainfall tended toward a higher species richness (Table 5). No effect of whether quadrats were located at the edge or in the centre of a vineyard block was observed in either the ordination or the regression models (Table 5).

Discussion

Our results indicated that weed community composition in Western Cape vineyards varies in association with different management practices and that weed communities found under different management practices vary in their competitive potential and value to biodiversity. In general, sites managed by mowing permitted a higher diversity and abundance of weeds, including more native weeds, to persist during winter to support biodiversity (Figs. 2 and 3). Tillage was effective to limit weed cover in summer, when competition for water is more critical in the Western Cape, and did not appear to adversely affect weed diversity or native weeds (Fig. 3). This suggests that managing weeds through a combination of mowing and tillage may be the best approach to optimise the balance between the value to biodiversity and the competitive potential of a weed community in Western Cape vineyards. In contrast, herbicide use was associated with reduced weed diversity and fewer native weeds and an intermediate weed cover in both summer and winter. These results support previous studies that also identified possibilities for management to promote optimal weed communities, with high value to biodiversity but low competitive potential, in other farming systems (Storkey, 2006; Storkey & Westbury, 2007; Mézière *et al.,* 2015; Fracchiolla *et al.,* 2015).

Management practices filter weed communities through removing species that do not have the requisite traits to survive those practices and thus may limit weed diversity (Gaba *et al.,* 2014). Where there are few species adapted to survive, stronger filters can also limit overall weed abundance, as evidenced by the higher efficacy of herbicides and tillage in reducing weed cover compared with mowing (Fig. 3). However, over time, these adapted species can increase in population. This study suggests that species known to be tolerant of herbicides, or prone to developing herbicide resistance, are increasing on conventional vineyards. For example, *Lolium* spp., a genus notorious for developing resistance to multiple herbicide mode-of-action groups (Heap, 2014), were associated with sprayed sites on conventional vineyards (Fig. 3). Weed species diversity and richness were also slightly lower in sprayed sites compared with mown and tilled sites (Fig. 3, Table 5), in agreement with numerous previous studies both in vineyards (Lososová *et al.,* 2002, Bruggisser *et al.,* 2010, Sanguankeo & León 2011) and in other farming systems (e.g. Fracchiolla *et al.,* 2016).

Declines in weed diversity with increased herbicide use has been explained by relatively few species possessing the requisite traits to survive herbicides (e.g. José-María *et al.,* 2010, Storkey *et al.,* 2010). This trend however is not universal, as for example an experiment by Gago *et al.,* (2007) on a Spanish vineyard indicated that weed species richness was similar between mown, tilled and sprayed treatments. The effect of a management action on diversity may therefore depend on how many resident species can tolerate that particular filter. In the Western Cape context, herbicides appear to limit weed diversity most strongly, and were also associated with reduced cover by native weed species (Fig. 3). Given that native plants are expected to have stronger relationships with native biodiversity at other trophic levels (McCary *et al.,* 2016), this can be expected to exacerbate the effect of weed diversity loss on the overall biodiversity of Western Cape vineyards.

The filtering effect of management actions on different weed traits can also shift weed functional community composition and this may further influence its relative competitive potential and value to biodiversity (Navas 2012, Gaba *et al.,* 2014). Agricultural practices that impose a high disturbance intensity on weeds, such as herbicides and tillage, have been previously observed to filter for weed communities with traits indicative of a ‘faster’ life strategy (, Storkey *et al.,* 2010, Navas 2012). ‘Fast’ species are typically resource-demanding (Reich 2014), which may result in increased sequestering of resources by weeds away from crops, including grapevines. This study assessed weed height, seed mass and SLA as indicators of weed life history strategy, with tall, small-seeded species with a high SLA (all ‘fast’ traits) expected to increase competitive potential with grapevines (see Table 2 and section *Weed community composition and characteristics*). Community-weighted means of all three traits varied in association with management practices (Figs. 2 and 3, Table 5). Specifically, tilled and sprayed sites tended to have taller weeds, a trait associated with increased competitive ability for both light and water (Violle *et al*., 2009). Tilled sites also tended to have a higher mean SLA, indicative of faster resource uptake and turnover (Kazakou *et al.,* 2016). Sites treated with herbicides tended to have small seeded weeds, which permit the production of a large number of successful offspring when resources are abundant and competition at the seedling stage is low (Westoby 1998, Garnier & Navas 2012). Overall, this suggests that the disturbance imposed by herbicides and tillage compared with mowing selects for a ‘faster’ life history. Mowing does not remove all biomass and thus may be more likely to select for species that conserve resources for recovery, rather than those that invest primarily in rapid growth and high reproductive output (Navas 2012, Reich 2014). Mowing would also select directly against tall species by being more likely to remove the growth point and/or a greater quantity of biomass from such species.

While higher disturbance in general may select for a ‘fast’ life history strategy, the type of disturbance can also select for specific traits that confer survival to that disturbance. For example, the lower SLA observed under herbicide treatment may be associated with decreased leaf permeability and reduced susceptibility to herbicides, while the larger seed mass observed at tilled sites can confer increased survival when buried through tillage (Armengot *et al.,* 2016). Such interactions between selection for general success in highly disturbed environments, combined with the specific selection pressures imposed by different disturbance types, may explain some of the inconsistency in functional responses observed in the literature. For example, in regard to tillage, our study agreed with Armengot *et al.,* (2016) who also found taller, larger-seeded weeds under increased tillage, and partially with Kazakou *et al.,* (2016) who found shorter weeds with a higher SLA in tilled sites. It disagrees with Fried *et al.,* (2012) who concluded that tillage promotes shorter, smaller-seeded weeds. It seems likely that different types, timings and intensities of tillage in different environments and in different combination with other management (e.g. herbicides) determine whether it is more advantageous for weeds to adapt specifically to tillage (larger seeds to survive burial) or to generally adapt to growing and reproducing between disturbance events (fast growth and production of many small seeds).

Our premise that a low SLA is more desirable than a high SLA amongst vineyard weeds is open to debate. Further research is needed to determine the conditions in which different resource economics traits such as SLA are associated with competitiveness in weeds. A high SLA is a ‘fast’ trait associated with rapid resource uptake, but species with such a strategy are less competitive when resources become limiting (Reich 2014). Thus they may have less impact on grapevines in the drier summer season than ‘slow’ species that persist and continue to compete at low water availability. Increased mortality of ‘fast’ species at low moisture may explain the low summer weed cover observed at tilled sites. In addition, plant species with a high SLA may be more beneficial to nutrient cycling and more valuable to other biodiversity than species (Storkey *et al.,* 2013, Kazakou *et al.,* 2016).

Weed community composition responds to environmental conditions, as well as to management (Hanzlik & Gerowitt, 2015), and in this study was observed to differ between drier areas with sandier soils low in nutrients and more humid areas with greater soil clay and silt content and higher nutrient availability (Fig. 2). Winter weed cover decreased as soils became sandier and species richness increased as rainfall increased. Environmental conditions may therefore constrain the degree to which farmers are able to select for desirable community characteristics. Furthermore, environmental conditions may determine which community characteristics are desirable, with ‘slow’ species potentially more competitive in arid or low-nutrient areas and ‘fast’ species posing a greater problem where resource availability is higher in the absence of competition (Reich, 2014). This could be explored in future research.

In contrast to other studies, we did not observe any difference between weed communities in the centre of vineyard blocks compared with the edge. Other studies suggest that dispersal of species is easier to field edges, and management is less intensive, which allows a greater diversity of species to persist in edges compared to centres, and that functional composition also differs (José-María *et al.,* 2010, José-María *et al.,* 2011). It is possible that in vineyards this effect is weaker, as the less intensively managed interrows may effectively extend ‘edge’ habitat into the centre of vine blocks.

Conclusion

This study indicated that specific management practices are stronger drivers of weed community composition and characteristics in Western Cape vineyards than either overall management strategy, environmental variables, or edge effects within a vineyard block.

Mowing, tillage and herbicides all apply different strengths and types of filter effects on the weed community. Thus these practices are a primary influence on which weed species survive and on which effects they will have on the surrounding agroecosystem (Lavorel & Garnier, 2002; Kazakou *et al.,* 2016). Based on our results, we recommend that in the Western Cape, mowing is used as the primary means of weed management throughout winter and tillage used if necessary in spring. Mowing appears able to sustain the benefits of winter weed cover, weed diversity and native weeds for biodiversity whilst promoting shorter weeds, which are expected to be less competitive. However, if competition for water is of critical concern, it may be necessary to use an additional method to limit summer weed cover. Our results suggest that tillage is preferable to herbicides for this purpose, as it was associated with the lowest summer weed cover and did not have adverse effects on weed diversity or native weeds. Using tillage only in spring and where necessary would minimise the risk of soil erosion linked to tillage (van Oost *et al.,* 2006).

This study demonstrated the utility of applying the response-effect trait framework to identify desirable characteristics of weed communities and to understand how management practices can promote these desirable communities in vineyards in the context of local conditions. Consistently trying to remove all weeds from farmland has been shown to be unsustainable. Instead, pathways must be identified to reduce weed control and to integrate the positive functions of weeds into agroecosystems. Our findings indicate that mowing in particular warrants further investigation as a technique to allow Western Cape vineyard farmers to address the dual goal of sustaining both biodiversity and grape production.

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References

ANNETT R, HABIBI HR & HONTELA A (2014) Impact of glyphosate and glyphosate-based herbicides on the freshwater environment. *Journal of Applied Toxicology* **34**, 458–479. DOI:10.1002/jat.2997

ARMENGOT L, BLANCO-MORENO JM, BÀRBERI P *et al*. (2016) Tillage as a driver of change in weed communities: A functional perspective. *Agriculture Ecosystems and Environment* **222**, 276–285. DOI:10.1016/j.agee.2016.02.021

ATWOOD D & PAISLEY-JONES C (2017) *Pesticides Industry Sales and Usage; 2008-2012 Market Estimates*. United States Environmental Protection Agency, Washington DC, USA.

BÀRBERI, P, BURGIO G, DINELLI G *et al*., (2010) Functional biodiversity in the agricultural landscape: Relationships between weeds and arthropod fauna. *Weed Research* **50**, 388–401. DOI:10.1111/j.1365-3180.2010.00798.x

BOLKER BM, BROOKS ME, CLARK CJ, (2008) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* **24,** 127–135. DOI:10.1016/j.tree.2008.10.008

BRUGGISSER, O., SCHMIDT-ENTLING, M. & BACHER, S., (2010) Effects of vineyard management on biodiversity at three trophic levels. *Biological Conservation* **143,** 1521–1528. DOI:10.1016/j.biocon.2010.03.034

CATALDO D, HAROON H, SCHRADER L, & YOUNG V (1975) Rapid colorometric determination of nitrate in plant tissue by nitrate of salicylic acid. *Communications in Soil Science and Plant Analysis* **6,** 71–80.

DIAZ S & CABIDO M, (2001) Vive la difference: plant functional diversity matters to ecosystem processes: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* **16,** 646–655. DOI:10.1016/S0169-5347(01)02283-2

FERRARA G, MAZZEO A, MATARRESE A, *et al.* (2015) Soil Management Systems: Effects on Soil Properties and Weed Flora. *South African Journal of Enology and Viticulture* **36,** 11–20.

FRACCHIOLLA M, TERZI M, FRABBONI L, *et al.* (2016) Influence of different soil management practices on ground-flora vegetation in an almond orchard. *Renewable Agriculture and Food Systems* **31,** 300–308. DOI:10.1017/S1742170515000241

FRIED G, KAZAKOU E, & GABA S (2012) Trajectories of weed communities explained by traits associated with species' response to management practices. *Agriculture, Ecosystems and Environment* **158**, 147–155. DOI:10.1016/j.agee.2012.06.005

GABA S, FRIED G, KAZAKOU E *et al.* (2014) Agroecological weed control using a functional approach: A review of cropping systems diversity. *Agronomy for Sustainable Development* **34,**103–119. DOI:10.1007/s13593-013-0166-5

GAGO P, CABALEIRO C & GARCÍA J (2007) Preliminary study of the effect of soil management systems on the adventitious flora of a vineyard in northwestern Spain. *Crop Protection* **26**, 584–591. DOI:10.1016/j.cropro.2006.05.012

GAIGHER R & SAMWAYS MJ (2010) Surface-active arthropods in organic vineyards, integrated vineyards and natural habitat in the Cape Floristic Region. *Journal of Insect Conservation* **14**, 595–605. DOI:10.1007/s10841-010-9286-2

GARNIER E & NAVAS ML (2012) A trait-based approach to comparative functional plant ecology: Concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable Development* **32**, 365–399. DOI:10.1007/s13593-011-0036-y

GRIME JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169–1194.

HANZLIK K. & GEROWITT B (2015) Methods to conduct and analyze weed surveys in arable farming. A review. *Agronomy for Sustainable Development* **36,** 11-29. DOI:10.1007/s13593-015-0345-7

HEAP I (2014) Herbicide resistant weeds. In *Integrated Pest Management; Pesticide Problems, Vol. 3* (eds D Pimental & R Peshin). Springer, Netherlands. DOI:10.1007/978-94-007-7796-5_12

JOSÉ-MARÍA L, ARMENGOT, L, BLANCO-MORENO JM, BASSA M & SANS FX (2010) Effects of agricultural intensification on plant diversity in Mediterranean dryland cereal fields. *Journal of Applied Ecology* **47**, 832–840. DOI:10.1111/j.1365-2664.2010.01822.x

JOSÉ-MARÍA L., BLANCO-MORENO JM, ARMENGOT L & SANS FX (2011) How does agricultural intensification modulate changes in plant community composition? *Agriculture, Ecosystems and Environment* **145**, 77–84. DOI:10.1016/j.agee.2010.12.020

KATTGE J, DÍAZ S, LAVOREL S, *et al*. (2011) TRY - a global database of plant traits. *Global Change Biology **17***, 2905–2935. DOI:10.1111/j.1365-2486.2011.02451.x

KAZAKOU E, FRIED G, RICHARTE J, GIMENEZ O, VIOLLE C & METAY A (2016) A plant trait-based response-and-effect framework to assess vineyard inter-row soil management. *Botany Letters* **163**, 373–388. DOI:10.1080/23818107.2016.1232205

KEENEY D & NELSON D (1982) Ammonium by colorimetric methods. In *Methods of Soil Analysis, Part 2; Chemical and Microbiological Properties* (eds A. Page, R Miller & D Keeney)*,* 2nd edn 643-698*.* American Society of Agronomy*,* Madison, Wisconsin USA.

LAVOREL S & GARNIER E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**, 545–556. DOI:10.1046/J.1365-2435.2002.00664.X

LEPŠ J & HADINCOVÁ V (1992) How Reliable Are Our Vegetation Analyses? *Journal of Vegetation Science* **3**, 119–124.

LOSOSOVÁ Z, DANIHELKA J & CHYTRÝ M (2002) Seasonal dynamics and diversity of weed vegetation in tilled and mulched vineyards. *Biologia* **57**, 47–55.

MARSHALL EJP, BROWN VK, BOATMAN ND, LUTMANS PJW, SQUIRE GR & WARD LK (2003) The role of weeds in supporting biological diversity within crop fields. *Weed Research* **43**, 77–89. DOI:10.1046/j.1365-3180.2003.00326.x

MCCARY MA, MORES R, FARFAN M AND WISE D (2016) Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: A meta-analysis. *Ecology Letters* **19**, 328–335. DOI:10.1111/ele.12562

MÉZIÈRE D, PETIT S, GRANGER S, BIJU-DUVAL & COLBACH N (2015) Developing a set of simulation-based indicators to assess harmfulness and contribution to biodiversity of weed communities in cropping systems. *Ecological Indicators* **48**, 157–170. DOI:10.1016/j.ecolind.2014.07.028

MORTENSEN DA, EGAN JF, MAXWELL BD, RYAN MR AND SMITH RG (2012) Navigating a Critical Juncture for Sustainable Weed Management. *BioScience* **62**, 75–84. DOI:10.1525/bio.2012.62.1.12

NAVAS ML (2012) Trait-based approaches to unravelling the assembly of weed communities and their impact on agro-ecosystem functioning. *Weed Research* **52**, 479–488. DOI:10.1111/j.1365-3180.2012.00941.x

OERKE EC (2006) Crop losses to pests. *The Journal of Agricultural Science* **144**, 31-43 DOI:10.1017/S0021859605005708

R CORE TEAM (2016) R: *A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/

REICH PB (2014) The world-wide “fast–slow” plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**, 275–301. DOI:10.1111/1365-2745.12211

SANGUANKEO PP & LEÓN RG (2011) Weed management practices determine plant and arthropod diversity and seed predation in vineyards. *Weed Research* **51**, 404–412. DOI:10.1111/j.1365-3180.2011.00853.x

SCHULZE RE (1997) *South African Atlas of Agrohydrology and Climatology.* Report No. TT82/96, Water Research Commission, Pretoria, South Africa.

STORKEY J, MOSS SR, & CUSSANS, JW (2010) Using assembly theory to explain changes in a weed flora in response to agricultural intensification. *Weed Science* **58**, 39–46. DOI:10.1614/Ws-09-096.1

STORKEY J, BROOKS D, HAUGHTON A, HAWES C, SMITH BM AND HOLLAND JM (2013) Using functional traits to quantify the value of plant communities to invertebrate ecosystem service providers in arable landscapes. *Journal of Ecology* **101**, 38–46. DOI:10.1111/1365-2745.12020

STORKEY J & CUSSANS JW (2007) Reconciling the conservation of in-field biodiversity with crop production using a simulation model of weed growth and competition. *Agriculture, Ecosystems & Environment* **122**, 173–182. DOI:10.1016/j.agee.2006.12.031

STORKEY J (2006) A functional group approach to the management of UK arable weeds to support biological diversity. *Weed Research* **46**, 513–522. DOI:10.1111/j.1365-3180.2006.00528.x.

VAN OOST K, GOVERS G, DE ALBA S & QUINE TA (2006) Tillage erosion: a review of controlling factors and implications for soil quality. *Progress in Physical Geography* **30**, 443–466. DOI:10.1191/0309133306pp487ra

VIOLLE C, GARNIER E, LECOUER J *et al* (2009) Competition, traits and resource depletion in plant communities. *Oecologia* **160**, 747–755. DOI:10.1007/s00442-009-1333-x

WESTOBY M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213–227.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Summary of management practices and mean community characteristics

Appendix S2: Checklist of weed species encountered in the surveys

TABLES AND CAPTIONS

Table 1 The Domin scale, a ten-point scale for visual estimation of percent cover of a quadrat with a higher resolution at lower covers. Domin scores are converted to their mid-point percent for the purpose of quantitative analyses (Lepš & Hadincová 1992).

Domin score	Percent cover band	Percent cover midpoint
1	rare	0.5
2	occasional	1.5
3	frequent	3
4	4-10	6.5
5	11-25	18.5
6	26-33	30
7	34-50	41.5
8	51-75	62.5
9	76-90	81.5
10	91-100	95

Table 2 A summary of the eight community characteristics indicative of value to biodiversity and of competitive potential with grapevines. Arrows indicate whether the relationships between community characteristics and biodiversity value or competitive potential are expected to be positive (upwards arrow) or negative (downwards arrow). (CWM = community-weighted mean, SLA = specific leaf area)

Community characteristic	**Biodiversity value**	**Competitive potential**
Winter weed % cover	⇧	
Summer weed % cover	⇧	⇧
Native weed % cover	⇧	
Species richness	⇧	
Shannon diversity	⇧	
Height CWM		⇧
Seed mass CWM		⇩
SLA CWM		⇧

Table 3 Environmental variables collected during the vineyard surveys

Variable	Abbrev.	Method
texture (sand, silt, clay content)	sand, silt, clay	Five soil sub-samples to 10cm depth were collected from the centreline of the quadrat and combined to form a single representative sample. Texture, pH, K and extractable P were determined using methods described by the Non-Affiliated Soil Analysis Work Committee (1990), while N content was determined using the indophenol-blue test for ammonium (Keeney & Nelson, 1982) and the salicylic acid method for nitrate (Cataldo *et al.,* 1975).
pH	pH	
nitrogen (N)	N	
phosphorus (P)	P	
potassium (K)	K	
average annual rainfall	rain	Obtained from data collected in Schulze (1997) of rainfall from 1950 to 1997 (while average rainfall may have changed since 1997, this average is still considered to provide a good estimate of relative differences in rainfall between vineyards).
elevation	elev	Recorded with a 'Garmin GPSmap 64s' handheld GPS device.

Table 4 The defining criteria to classify vineyards into different management strategies, and the common management practices observed under each management strategy

Management strategy	Defining criteria for management strategy	Common management practices
Organic	No chemical herbicides No chemical fertilisers Certified to or in conversion to EU organic standards	Tillage, mowing
Low-input	Maximum one application of glyphosate only per year Manure or compost-based herbicides only	Tillage, mowing, herbicides
Conventional	Multiple herbicide applications and/or multiple herbicide mode-of-action groups Various fertiliser types including chemical fertilisers	Tillage, mowing, herbicides

Table 5 ANOVA F statistics and *P*-values (based on Satterthwaite Type 3 F tests) for the fixed effects in the mixed models of each community characteristic against management and key environmental variables (these models included with quadrat nested in block nested in vineyard as random effects). Symbols next to the *P*-values highlight significance at *P*<0.05 (*) or *P*<0.1 (º)

WINTER WEEDS % COVER	*ANOVA F statistic*	*P-value*
Vineyard block edge/centre	1.584	0.212
Soil sand % content	7.378	0.012 *
Annual rainfall	3.250	0.113
Management strategy	7.554	0.015 *
Management practices	5.476	<0.001 *
SUMMER WEEDS % COVER	*ANOVA F statistic*	*P-value*
Vineyard block edge/centre	0.000	0.994
Soil sand % content	0.329	0.569
Annual rainfall	1.519	0.259
Management strategy	1.799	0.226
Management practices	5.463	<0.001 *
NATIVE WEEDS % COVER	*ANOVA F statistic*	*P-value*
Vineyard block edge/centre	1.062	0.306
Soil sand % content	0.082	0.776
Annual rainfall	2.322	0.156
Management strategy	1.837	0.202
Management practices	4.185	0.002 *
SHANNON DIVERSITY	*ANOVA F statistic*	*P-value*
Vineyard block edge/centre	0.994	0.322
Soil sand % content	0.006	0.939
Annual rainfall	1.595	0.232
Management strategy	1.218	0.330
Management practices	2.688	0.025 *
SPECIES RICHNESS	*ANOVA F statistic*	*P-value*
Vineyard block edge/centre	1.782	0.186
Soil sand % content	0.118	0.732
Annual rainfall	8.616	0.013 *
Management strategy	3.236	0.076 º
Management practices	0.765	0.577
HEIGHT CWM	*ANOVA F statistic*	*P-value*
Vineyard block edge/centre	0.581	0.449
Soil sand % content	0.846	0.363
Annual rainfall	3.011	0.115
Management strategy	0.510	0.616
Management practices	2.536	0.035 *
SEED MASS CWM	*ANOVA F statistic*	*P-value*
Vineyard block edge/centre	2.126	0.148
Soil sand % content	0.740	0.395
Annual rainfall	1.408	0.259
Management strategy	2.150	0.155
Management practices	5.815	<0.001 *
SLA CWM	*ANOVA F statistic*	*P-value*

Vineyard block edge/centre	1.586	0.214
Soil sand % content	0.082	0.776
Annual rainfall	0.856	0.374
Management strategy	0.438	0.657
Management practices	3.180	0.014 *

FIGURES AND CAPTIONS

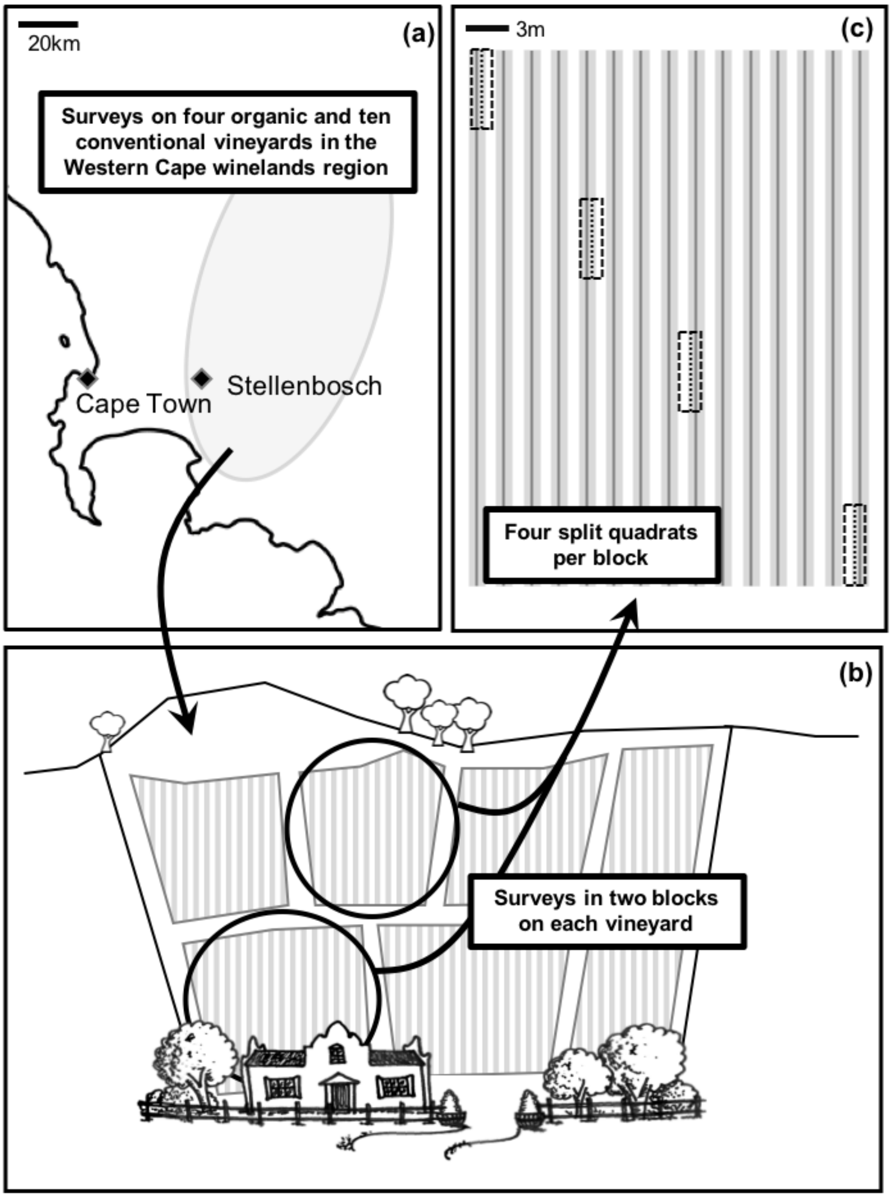

Fig. 1 An illustration of the study layout: (a) the area of the Western Cape in which vineyards included in this study were located, (b) on each vineyard weed communities were surveyed in two vineyard blocks, and (c) the layout of survey split-quadrats (dashed black) in each block, with vine rows shown as dark lines, the vine-row area shaded in grey, and the inter-row space is white.

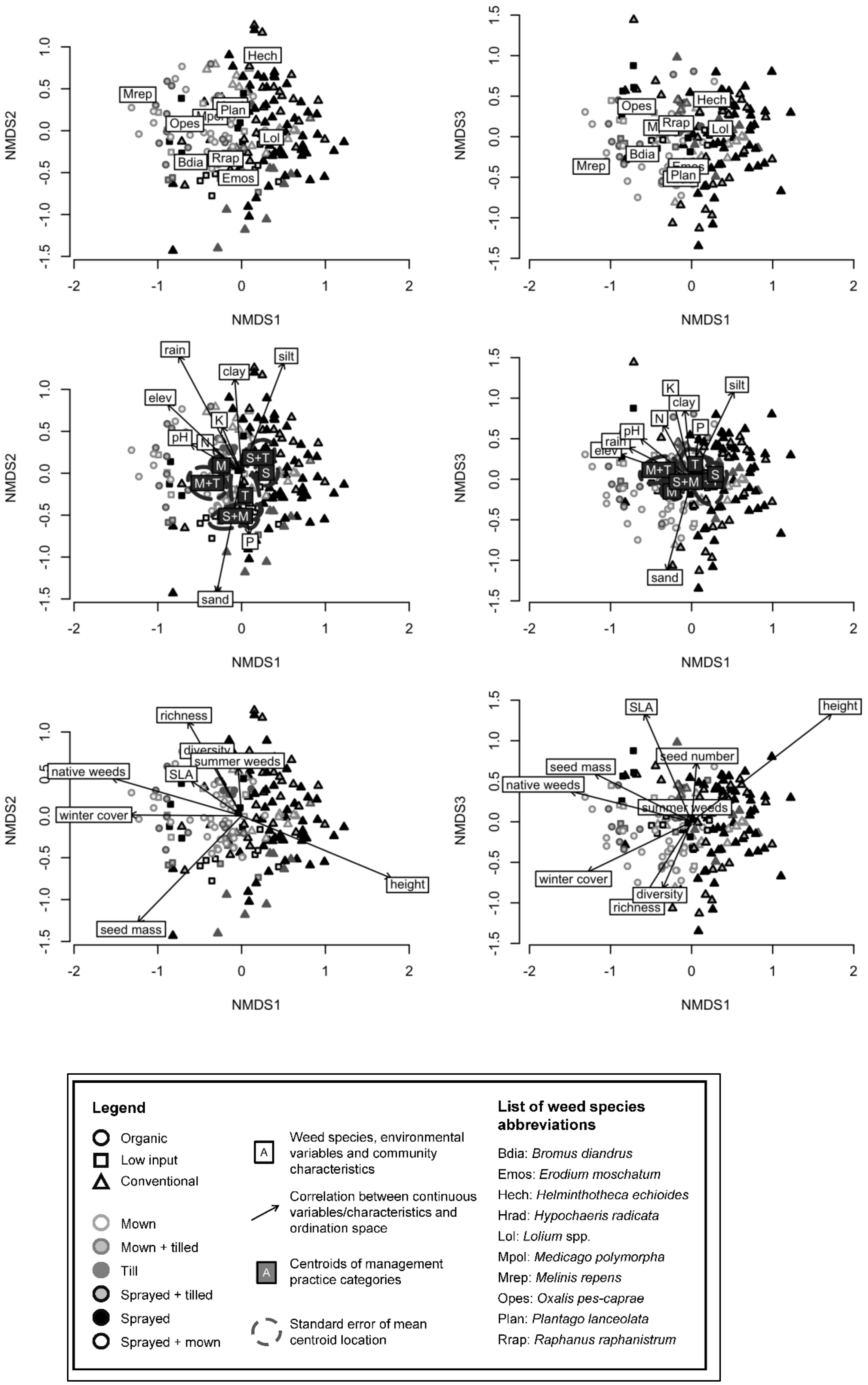
NMDS1
NMDS2
NMDS3
-2
-1
0
1
2
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Hech
Mrep
Plan
Mpol
Opes
Lol
Bdia
Rrap
Emos
rain
silt
clay
elev
K
pH
N
M
S+T
S
M+T
T
S+M
P
sand
richness
diversity
summer weeds
native weeds
SLA
winter cover
height
seed mass
seed number
Legend
Organic
Low input
Conventional
Mown
Mown + tilled
Till
Sprayed + tilled
Sprayed
Sprayed + mown
A
Weed species, environmental variables and community characteristics
Correlation between continuous variables/characteristics and ordination space
Centroids of management practice categories
Standard error of mean centroid location
List of weed species abbreviations
Bdia: Bromus diandrus
Emos: Erodium moschatum
Hech: Helminthotheca echioides
Hrad: Hypochaeris radicata
Lol: Lolium spp.
Mpol: Medicago polymorpha
Mrep: Melinis repens
Opes: Oxalis pes-caprae
Plan: Plantago lanceolata
Rrap: Raphanus raphanistrum

Fig. 2 The three-dimensional NMS ordination, with the position of sites along axes 1 and 2 displayed on the left, and axes 1 and 3 on the right. Points represent weed communities in each quadrat: different shades indicate different management practices, and shapes indicate management strategy. The top plots display common species in relation to overall community composition, based on weighted averages in ordination space (in both *Hypochaeris radicata* ‘Hrad’ is obscured by *Plantago lanceolata,* ‘Plan’). The centre plots illustrate the fitted vectors for environmental variables (arrows and white labels) and the centroids of different groups of management practices (dark labels). Dashed circles indicate the standard error of the management centroid mean: where circles do not overlap, community composition is significantly different between practices. The lower plots illustrate the fitted vectors of community characteristics.

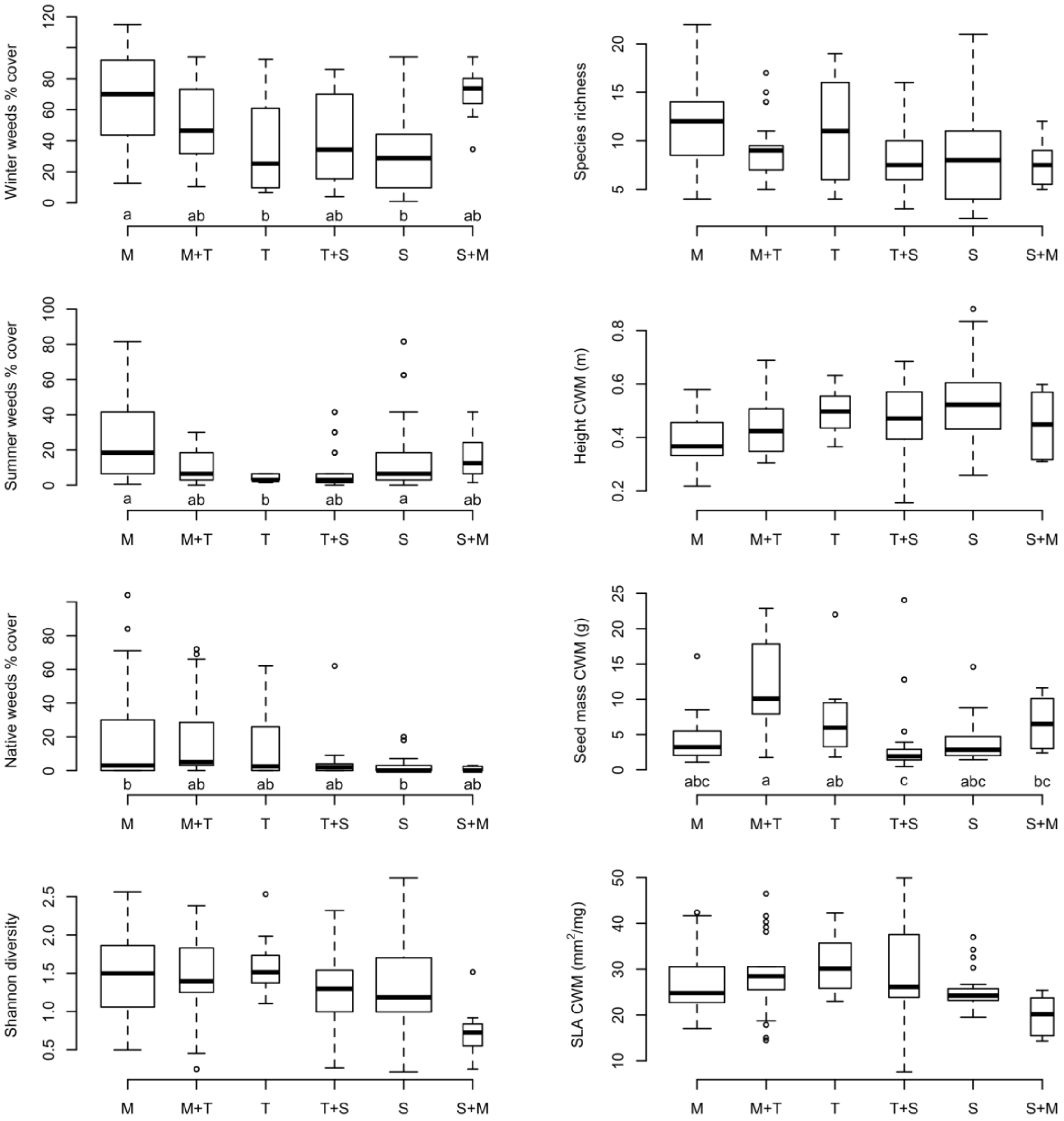

Fig. 3 Weed community characteristics under different management practices: M = mown, T = tilled, S = sprayed, and combinations thereof. Boxplot centre bands indicate the median, the box represents the interquartile range, the whiskers 1.5x the interquartile range (or the minimum/maximum where these fall inside that limit), and open points indicate outliers. Where lowercase letters are present under the boxes, this indicates that significant pairwise differences between management categories were identified based on the fixed effects set out in Table 5.