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Exploring the ecological intensification of weed management in cropping systems of South Africa's winter rainfall region

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Exploring the ecological intensification of weed management in cropping systems of South Africa's winter rainfall region

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ABSTRACT

Taking an ecological intensification approach to weed management could increase agriculture’s ability to meet human needs for food, fuel and fibre whilst avoiding impacts on the integrity of Earth’s life-supporting ecosystems. Ecological intensification would achieve this by replacing anthropogenic inputs with ecosystem function. In this thesis, ecosystem processes are sought that could replace conventional weed control inputs and actions such as herbicides and tillage, and so reduce the environmental impacts associated with these. First, there is a need to shift thinking away from isolated mechanisms that seek to remove weeds, and to instead aim for ‘agroecosystem resilience to weeds’ in which farming systems would be designed to incorporate ecological processes and properties that inherently limit the negative impacts and promote the positive roles of weeds. To understand how this resilience could be achieved, recent advances in weed ecology are reviewed to identify relevant processes and properties, and to consider how these might be implemented in farm design and management. In sum, practices that could increase the diversity of filters applied to weed communities while decreasing filter strength, and that could reduce resource availability, would be expected to confer agroecosystem resilience to weeds.

This thesis explores the practical implementation of some of these practices in South Africa’s winter rainfall region through field studies and trials. The practices were chosen for their suitability for conservation agriculture systems (the dominant farm management style in the region) and for their potential to harness or enhance ecological processes for weed management. The first practical study, a field survey of weeds in 15 vineyards with differing weed management practices, confirmed that the use of management techniques imposing lower disturbance leads to more diverse weed communities composed of less competitive species, and this effect can be enhanced by using specific management techniques to select for specific weed traits. The second practical study was linked to a long-term crop rotation experiment, and explored the effects of increasing crop diversity and integrating livestock as methods to increase the variability experienced by weeds in these rotation systems. Combining these two practices substantially reduced weed abundance and conserved weed diversity over the twelve years investigated. They also reduced herbicide and fertiliser requirements, and sustained cash crop yields, thus contributing to both profitability and sustainability. The final practical study applied theories of biotic resistance from invasion ecology to investigate how best to design cover crop mixes for weed suppression, that could be used in field crop systems or vineyards. Mixes composed of highly productive species were most effective at resource capture, and thus most effective at reducing resource availability to suppress weeds. In sum, reducing herbicide use in favour of grazing or mowing, increased crop and management diversity, and competitive crops (in mixes or monoculture) are viable practices that constitute first steps toward the ecological intensification of weed management in South Africa’s winter rainfall region. They offer improvements to agricultural sustainability through sustaining yields and farm incomes whilst reducing the environmental impacts and health risks associated with conventional weed control such as herbicides and tillage. Overall, the findings of this thesis suggest that ecological intensification offers a promising direction for future weed management to achieve agricultural sustainability, both in South Africa’s winter rainfall region and around the world. Weed researchers can assist farmers in this challenge by drawing on global advances in weed ecology to design and test locally appropriate weed management techniques and strategies.

CONTENTS

CHAPTER 1: INTRODUCTION

1.1 Weeds and weed management

A weed can be defined as ‘a plant out of place’ (Zimdahl 2013). Plants are considered ‘out of place’ when they grow where they interfere with human activities (WSSA 2016, EWRS 2017), or in ecosystems outside their native range (Richardson et al 2000). In the context of agriculture, a ‘weed’ can be defined as any plant that is undesirable in a particular location on a farm. Agricultural weeds can be either native or alien, although an alien agricultural weed could be considered doubly ‘out of place’ due to being both undesirable on the farm, and a potential threat to local natural ecosystems (Booth et al 2003, Pimentel et al 2005).

Plants become undesirable on farms when they grow in locations where they interfere with production through competing with crops, suppressing crops through allelopathy, harbouring pests and diseases, presenting toxicity risks to livestock, or interfering with farm management activities (Booth et al 2003, Zimdahl 2013). Of these, competition poses the greatest threat: if weeds are left unmanaged within crop fields then it is predicted they would cause yield losses of up to 34% in major crops worldwide, posing a greater threat to productivity than either animal pests or pathogens (Oerke 2006). For hundreds of years tillage has been used to remove weeds to counter these potential losses, and today over USD$ 20 billion are spent each year on more than 1.2 million tons of herbicide worldwide (Atwood and Paisley-Jones 2017).

However, there is increasing evidence that agricultural weeds may be less ‘out of place’ than has conventionally been supposed, and that weeds in cropped fields play beneficial as well as negative roles in agricultural production. Weeds support farmland biodiversity (Marshall et al 2003, Gurr et al 2003), including biodiversity beneficial to farm productivity, and can also contribute to sustaining soil quality (Blaix et al 2018). In some cases these effects result in weeds contributing to increased crop yields, for example through increasing beneficial soil organisms

(Feldmann and Boyle 1999, Blaix et al 2018). It is also becoming obvious that weed control actions including tillage and herbicides can degrade soil (van Oost et al 2006), pollute off-farm ecosystems and reduce their biodiversity (Relyea 2005, Annett et al 2014), and pose risks to human health (Mamane et al 2015, Myers et al 2016). Thus, the long-term costs of weed management may outweigh short-term yield benefits, if weed management is conducted in a way that does not take into account the positive roles of weeds and costs of weed control.

These long-term costs are becoming increasingly apparent to farmers, to the public and to policymakers. This is evidenced by increasing demand for organic produce and recent discussions around banning widely-used herbicides such glyphosate (Reganold and Wachter 2016). There has also been a shift in farming practices in many regions around the world to minimum tillage, in which ploughing is excluded from farm management and soil disturbance reduced as much as possible, with the aim of promoting soil organic matter sequestration and reducing soil erosion (Hobbs et al 2008). However, very few farmers have managed to achieve 'organic no-till' farming (Lègere et al 2013, Lehnhoff et al 2017). Currently, only a limited number of alternatives to tillage and herbicides for weed control exist, and often there is either insufficient knowledge or difficulties adapting these to the wide variety of agricultural systems and socioeconomic and pedoclimatic conditions around the world (Bajwa et al 2015, Liebmann et al 2016). To avoid reliance on damaging weed control practices, there is therefore a need for research that seeks both to identify novel approaches, and to adapt existing but under-utilised practices to new regions and new farming systems. It is also important that such research is grounded in a comprehensive understanding of sustainability, to ensure that any new practices will not generate long-term problems of their own.

1.2 Achieving sustainable weed management

Sustainability in agriculture

Weed management is just one of many activities undertaken for the purposes of agricultural production, and thus to understand what sustainable weed management would look like, it is first important to consider the sustainability of agriculture as a whole. The purpose of agriculture is to produce food, fuel and fibre to support human survival and quality of life, and so the fundamental goal of sustainable agriculture must be achieve this without undermining the capacity of future generations to meet those same needs (WCED 1987). However, this goal becomes self-defeating when production is obtained at the expense of other requirements for human survival and quality of life. Although conventional modern agriculture has increased production of food, fuel and fibre substantially over the past century, the severity of its impacts on the ecosystems that provide other life-supporting functions to humanity make it highly unsustainable (Tilman et al 2002). The economics of conventional agriculture also limit its sustainability, as the high dependence on inputs and high product specialisation limit the resilience of farmers and rural communities to both environmental and economic shocks (Cabell and Oelofse 2012).

The expansion and intensification of agriculture worldwide has been linked to disruption in the regulation of local and global climates and hydrological cycling, degradation in water quality, and loss of habitat for the enormous variety of other species that humans depend upon and share our world with (Tilman et al 2002, Foley et al 2005, Tscharntke et al 2012). In addition, modern agriculture has inhibited its own future potential to supply humankind with food, fuel and fibre. It has degraded soil quality and function (Pimentel et al 1995), and many of the amendments relied upon to sustain production are finite and in ever dwindling supplies (Cordell et al 2009). Attempts to protect crops from pests often harm other species that production relies on, such as the widespread use of neonicotinoids leading to declines in pollinators (Woodcock et al 2017).

To achieve its fundamental goal of sustaining human survival and quality of life, agriculture must therefore produce sufficient food (and fuel and fibre) without compromising its own future productivity or other life-supporting ecosystem services. Both of these depend on functioning ecosystems, and so to be sustainable, agriculture needs to operate within biophysical boundaries that conserve

Figure 1.1: An adaptation of Raworth's (2012) concept of sustainability, illustrating that the 'safe and just space for humanity' lies between exploiting natural resources sufficiently to meet our needs and welfare, but avoiding over-exploitation that leads to exceeding the biophysical boundaries of ecosystem integrity (discussed in Rockström et al 2009 and Steffen et al 2015). The text in the lower part of the figure illustrates that 'the safe and just space for humanity' can be achieved by designing farming systems that are able to both provide adequate food fuel and fibre whilst conserving biodiversity, natural habitat and ecosystem functioning.

ecosystem integrity (Foley et al 2005, Steffan et al 2015, Rockström et al 2017). This dual need to produce food whilst conserving ecosystem integrity can be best envisaged using Raworth's (2012) concept of sustainability (Figure 1): we should utilise the natural environment sufficiently to sustain our lives and wellbeing, but not so much as to threaten the continued functioning of the ecosystems that we rely on. Raworth succinctly states this as "meeting the needs of all within the means of the planet". It can also be argued that there is an intrinsic right of the multitude of other species we share the planet with to continue their lives undisturbed by human activity, and that there is also a moral imperative to minimise the impacts of our activities on their existence (Oksanen 1997).

The challenge of sustainability is to stay within Raworth's conceptual 'just and safe space for humanity' (Figure 1), to meet human needs without degrading the environment. In the context of agriculture, it has been proposed that we should follow a path of 'sustainable intensification' (Jordan and Davis 2014, Garnett et al 2016), in which methods are sought that can increase or sustain agricultural yields whilst reducing the inputs applied. This necessitates increasing resource use efficiency and retaining more resources with agricultural systems, and thus reduces the environmental impacts of resource acquisition and resource loss as pollution. Whilst this can present a step toward minimising the environmental impacts of agriculture, this concept of 'sustainable intensification' has been criticised for using an insufficiently rigorous definition of sustainability. It has thus been easy to co-opt for the purposes of marketing products and technology that offer marginal improvements in resource efficiency, without sufficiently addressing the environmental and social challenges faced by agriculture and rural communities (Tittonell 2014, Pimbert 2015, Wezel et al 2015). Increased resource efficiency can also result in Jevon's paradox or the 'rebound effect', where increased efficiency leads to lower relative cost of the resource and thus an increased demand for and use of the resource (Alcott 2005).

In response to such criticisms, 'ecological intensification' has been proposed as more robust pathway to agricultural sustainability (Doré et at 2011, Tittonell and Giller 2013, Tittonell 2014). Ecological intensification of agriculture can be defined as the "the replacement of anthropogenic inputs and/or enhancement of crop productivity, by including regulating and supporting ecosystem services management in agricultural practices" (Bommarco et al 2015). This approach not only reduces resource acquisition and losses from the system, but also actively seeks to work with the natural world to meet our needs, which explicitly requires that we do not push it beyond its limits in doing so (Doré et al 2011, Bommarco et al 2015). A recent paper by Rockström et al (2017) has brought the concepts of sustainable intensification and ecological intensification back together by arguing that the only way in which agriculture can be intensified in a truly sustainable manner is through the use of ecosystem processes. The concept is also similar to ‘agroecology’, and can be considered synonymous with the science and production practice aspects of agroecology (Tittonell 2014, Wezel et al 2015).

There is increasing evidence to suggest that ecological intensification can offer substantial progress in moving agricultural systems toward the ‘safe and just space for humanity’. Farming practices that reduce dependence on agricultural inputs such as fertilisers and pesticides by increasing within-farm diversity and ecosystem functioning can lead to substantial improvements in sustaining agricultural production and farm livelihoods, as well as in wider biodiversity and ecosystem functioning (Altieri 2002, Kremen and Miles 2012, Tittonell and Giller 2013, Altieri et al 2017). From an environmental perspective, substituting inputs for ecosystem functions avoids the impacts associated with inputs, and also tends to rely on ecosystems and species assemblages being at least partially protected or restored to perform their function (Tscharntke et al 2012, Bommarco et al 2015). This can have additional environmental benefits through the support of species or provision of function that benefit non-farmed biodiversity as well as agroecosystems. From a social perspective, more diverse and autonomous agroecosystems are typically more resilient, provide more reliable yields, and support a higher quality of life for rural communities (Altieri 2002, Tscharntke et al 2012, Cabell and Oelofse 2012, Tittonell and Giller 2013). Overall, the evidence so far suggests that ecological intensification is the most promising way forward to return agriculture to the ‘safe space’ of sustainability, in which it can meet our food, fuel and fibre needs without compromising other requirements for our survival and wellbeing.

Ecological intensification for sustainable weed management

The conventional aim of weed management has been to prevent weeds competing with crops or interfering with farm operations through eliminating weed biomass and preventing weed reproduction. Overwhelmingly, the tools recruited for these purposes are herbicides and tillage

(Zimdahl 2013). This approach to weed management reflects the focus of most modern agriculture on increasing immediate production, with little consideration given to either future productivity or the environment. Regular and intensive use of either herbicides or tillage or both is associated with soil erosion (Montgomery 2007, Keestra et al 2016), environmental pollution and biodiversity loss (Gaba et al 2015, Van Dam et al 2015, Verheijen et al 2009), risks to human health (Mamane et al 2015, Myers et al 2016), and long-term degradation in soil function and fertility (Hobbs et al 2006, Druille et al 2013, Lal 2015). Heavy reliance on herbicides also tends to promote herbicide resistance in weeds, which limits the lifespan of their utility in contributing to agricultural production (Neve et al 2009, Mortensen et al 2012).

These negative effects of conventional weed management all essentially result from failing to consider the long-term interactions between weeds, weed control actions, and the agroecosystem (Bàrberi 2002). In contrast, ecological intensification offers a sound approach to meet the challenge of understanding and managing these interactions. It is the study of ecology that has informed us of the biophysical planetary boundaries and the processes by which human activities cause these to be exceeded (Rockström et al 2009, Steffan et al 2015, Weiner 2017), and likewise it is ecology that describes the dynamics of weed populations and communities in time and space (Booth et al 2003, Davis 2017). Ecology therefore provides the key to identifying which management approaches have potential to limit the negative impacts of weeds on agriculture whilst remaining within the ‘safe space’ of global planetary boundaries. Furthermore, processes that operate in natural ecosystems to limit population abundance and promote plant co-existence offer a blueprint for designing agroecosystems that limit weed numbers and competition with crops, whilst promoting their diversity and contributions to ecosystem services (Neve et al 2009, Smith 2015, Storkey and Neve 2018). The ecological intensification of weed management would be the act of putting this into practice.

To some extent, ecological intensification is already present in weed management. For example, both crop rotation and intercropping rely on ecological interactions between plants and their conditions in space and time to limit weeds. However, although these practices have formed part of the weed management literature for decades (e.g. Swanton et al 1991, Liebmann and Dyck 1993), they remain under-utilised in farming systems around the world (Liebmann et al 2016; some reasons for this will be discussed below). Meanwhile, few novel practices based on ecological processes or relationships have since been added to the weed management repertoire. Recent reviews of weed management research still focus on chemical and mechanical interventions (Shaner and Beckie 2014, Bajwa et al 2015, Westwood et al 2018). Progress in ecological weed research appears to be inhibited by an over-allocation of funding and research effort toward 'weed control', primarily chemical or mechanical removal of weeds, and a neglect of integrated management strategies. In the view of Harker and O'Donovan (2013), this "continues to retard the development of weed science as a balanced discipline".

Several authors have also identified a divide in weed science between 'weed biology' and 'weed management' (Fernandez-Quintanilla et al 2008, Ward et al 2014, Neve et al 2018). This is perhaps a reflection of the dichotomy that weeds can impose strong negative effects on crops, yet also provide important ecosystem functions within agricultural landscapes. As described by Ward et al (2014), weed researchers typically focus on either fundamental weed ecology with the aim of understanding (and often conserving) weeds (e.g. Storkey et al 2010, Navas 2012), or on applied techniques for weed control, with the aim of removing weeds from farming systems (e.g. Westwood et al 2018). Neve et al's (2018) horizon-scanning exercise in weed science also found that "almost all the challenges identified rested on the need for continued efforts to diversify and integrate agroecological, socio-economic and technological approaches in weed management". The lack of efforts to integrate weed biology and weed management has largely left ecologists reprimanding weed managers for pursuing unsustainable practices (e.g. Gaba et al 2016), while managers evidently do not appreciate the potential of ecology to underpin sustainable weed management strategies (e.g. Westwood et al 2018).

Currently, even where 'ecological' techniques are described in the context of applied weed management, they are often simply reduced to additional control techniques, such as introducing biocontrol agents or bioherbicides (Bajwa et al 2014). This ignores the primary contribution that ecology can make to weed management in revealing how weeds interact with agroecosystems and farm management, and thus to identify possibilities for systems-level integrated management strategies that would be both effective and sustainable. For example, there is no research to suggest that weeds will not be just as capable of evolving resistance to bioherbicides (Neve et al 2009), nor that applying unnaturally high concentrations of these ‘natural’ chemicals to landscapes will not also have negative impacts on biodiversity and soil functioning. In contrast, ecological intensification offers a route to explicitly centralise the role of systems-level ecology as the basis for weed management strategies, and to encourage more communication between weed ecologists and weed managers. Ecologists will need to understand more about management to direct their work to meet its needs and constraints, whilst an increased understanding of ecology would allow weed managers to explore new options that rely less on unsustainable inputs, and that are less likely to promote long-term complications such as resistance.

One reason that research on herbicides and tillage has previously dominated the weed management agenda may be because these techniques are relatively simple, and applicable to many regions with only minor modifications. In contrast, ecological intensification is complicated by needing to work with organisms and processes that can survive in and are suitable to the agroecosystem in question. Different climatic and soil conditions in different parts of the world result in different ecosystem structures, and thus ecological intensification strategies will need to be informed by processes and conditions in local ecosystems (Ewel 1999, Bommarco et al 2015). Furthermore, these will need to work with locally available tools and be appropriate for local socioeconomic conditions (Doré et al 2011, Cunningham et al 2013). Such specificity is common to all applications of ecological intensification in agriculture, where embracing ecological complexity demands local solutions to local problems.

The need for locally adapted solutions may be a reason why ecological weed management strategies that are well documented in the scientific literature have not been widely adopted around the world. A simple example is integrated weed management (IWM), an approach in which multiple weed control techniques are used to avoid weeds developing tolerance or resistance to any single technique. However, as Harker and O'Donovan (2013) point out, in practice this often results in farmers applying 'integrated herbicide management' and varying weed management only through varying different herbicide mode-of-action groups. This does not achieve the environmental benefits that would result from reducing herbicide use in a more diverse IWM strategy, and given the increasing spread of multiple resistance becoming problematic in weed species around the world (Heap 2014), it seems that this may also not be able to achieve successful weed suppression for much longer. IWM typically becomes 'integrated herbicide management' in systems that have minimised soil tillage, often for sound environmental and productivity reasons such as reducing soil erosion and building soil carbon content. In such systems, weed management becomes a challenge due to the absence of tillage as a weed control method (Chauhan et al 2012, Bajwa 2014). Thus, for farmers using zero tillage practices, to implement successful IWM, additional alternatives to both herbicides and tillage need to be made available.

It is argued by many authors that a major barrier to sustainable agricultural practices, in general (Pretty et al 2011, Rockström et al 2017) or specifically for weed management (Jordan et al 2016, Liebmann et al 2016), is the constraints imposed by the political and socio-economic environment. For example, crop rotation diversity is often limited by a lack of markets or by subsidies given for particular crops. These authors therefore recommend a greater research focus on socioeconomics and policy in research toward agricultural sustainability, as favourable policies and infrastructure could incentivise the rapid uptake of sustainable practices. However, investigating possibilities to introduce sustainable farming techniques *within* the constraints of current systems would also allow steps to be taken toward sustainability regardless of progress in political change, and this may hasten overall progress toward sustainability. Furthermore, ecological intensification based in on-farm ecological functioning provides a potential path toward developing production techniques that empower farmers to become more autonomous and independent of input providers. The need for local solutions to local problems under ecological intensification, although an impediment to developing broad-scale solutions, may be advantageous in enabling farmers to reclaim sovereignty over their systems and rely less on 'one-size-fits-all' solutions from external suppliers (Altieri 2002, Altieri et al 2017). In addition to the environmental and long-term productivity benefits, reducing reliance on inputs would reduce consumption of inputs and thus the global profit potential and power of the input markets. In that sense, field scale initiatives toward sustainable agriculture may also help to facilitate political and economic shifts.

In terms of progressing toward sustainable weed management, there is therefore a need to design ecological intensification strategies that suit the variety of farming systems and environmental and socioeconomic conditions around the world. Weed researchers have a key role to play in assisting farmers in addressing this challenge, through using their access to scientific knowledge to draw on global advances in ecological theory and weed science to design and test locally appropriate management techniques and approaches (Anderson et al 2005, Jordan et al 2016, Liebmann et al 2016). Adapting ecological theory to farm practice is not always straightforward, and given the risks involved, many farmers prefer to adopt new ideas only after having seen them successfully implemented in their own environments and farming systems. For example, this is seen in the increased adoption of new practices amongst farmers whose neighbours and social networks have previously adopted the practices (Ward and Pede 2014, Läpple and Kelley 2015). Weed researchers can help to introduce new practices by piloting potentially suitable approaches on demonstration farms, and ensuring that results are both accessible and relevant to farmers (Payne et al 2016, Liebmann et al 2016).

Local trials of new ideas and practices can therefore present a key first step in the introduction and upscaling of ecological intensification in a region. This thesis takes this approach to explore possibilities for the ecological intensification of weed management in cropping systems of South Africa's winter rainfall region. It follows a process of drawing together theories from weed ecology that could underpin the ecological intensification of weed management, then trials the application of practices informed by these theories to the region's specific context. South Africa's winter rainfall region presents a unique set of challenges to weed management, against which ecological intensification approaches can be evaluated in terms of their capacity to meet the multiple needs of sustainably securing food production and farm incomes whilst also protecting biodiversity and ecosystem integrity.

1.3 Ecological intensification for weed management in South Africa’s winter rainfall region

An overview of farming systems in South Africa’s winter rainfall region

South Africa’s winter rainfall region is located in the southwest of the Western Cape Province (Figure 1.2). Precipitation ranges from approximately 200 mm per year in the northern Swartland to 1200 mm in parts of the Winelands (Schulze 2009). Agricultural systems in the region consist primarily of field crops in the Southern Cape and the Swartland, and of vineyards and fruit orchards in the Wineland region (Figures 1.3 and 1.4). The field crops are typically cereals including wheat *(Triticum aestivum),* oat *(Avena sativa),* and barley *(Hordeum vulgare),* which are often rotated with the canola *(Brassica napus).* On some farms, these are also rotated with legumes, such as lupins *(Lupinus* spp.*)* as a cash crop for animal feed, and lucerne *(Medicago sativa)* or annual medics *(Medicago* spp.) for hay or as a grazed annual pasture.

The ‘winter rainfall region’ is so named as it is the only part of the South Africa in which the majority of rain (60-80%) falls in the winter, between April and September (Hardy et al 2011). Due to this rainfall distribution, vineyards and orchards are often irrigated in spring and summer to ensure adequate production. Rainfed agriculture is only possible during the winter months, so in the small grain systems, only one crop can be planted each year: crops are typically sown in April and harvested in late November. Fields are left fallow over the summer, except in parts of the Southern Cape where summer rainfall is sufficient to sustain lucerne *(Medicago sativa)* as a perennial forage. Lucerne is used as a five-year perennial ley in rotation with annual small grain crops, and is either grazed or cut for hay. Work is also beginning on identifying annual cover crops that are viable to grow over the summer in the Southern Cape, but these are not yet widely used.

Figure 1.2: Map showing South Africa within Africa, and the municipalities (bold lines) and districts (narrow lines) of the Western Cape. The dashed blue line indicates the approximate area considered the ‘winter rainfall region’, or the area that receives at least 200mm rain per year, of which over 50% falls in the winter. Relevant agricultural regions are identified with labels (see main text). *Image source:* Wikimedia Commons.

Figure 1.3: Vineyards on the slopes of Simonsberg, in the Winelands of South Africa’s winter rainfall region.

Figure 1.4: Field cropping systems in South Africa’s winter rainfall region. *Top:* sheep graze an annual medic pasture *(Medicago truncatula* or *Medicago polymorpha)* in early winter, with canola and wheat crops visible in the background. *Bottom:* wheat shortly before harvest in spring, with canola, wheat and medic visible in other fields in the background.

The commercial small grain systems in South Africa’s winter rainfall region have developed from primarily monoculture wheat systems, which were established by early European settlers and constrained by regulations and targeted subsidies well into the 1900s (see Swanepoel et al 2015). Some diversification of cropping systems occurred in the 1950s along with a set of soil conservation measures aimed at addressing high rates of soil erosion observed in the 1930s and 40s (Meadows 2003). In the 1980s, efforts were made to introduce annual medic *(Medicago* spp.) pastures and multi-year lucerne leys to raise sheep in rotation with wheat, and to reduce the long-term declines in wheat yields attributable to problems associated with monocultures. However, the greatest changes in these systems occurred following the end of apartheid and the end of the associated international sanctions in the 1990s. During apartheid domestic wheat production was protected and subsidised, but in the 1990s subsidies ended, and the wheat market was deregulated and the farmers exposed to world markets. This further reduced profit margins for wheat and incentivised farmers to further diversify their cropping systems through crop rotation (Swanepoel et al 2015). Canola was introduced during the 1990s and continues to form a profitable element of commercial cropping systems (PRF 2016), alongside medic and lucerne pastures either grazed or harvested for hay (Swanepoel et al 2015). The production of lupins for animal feed was also increased during the 1990s, although due to problems with pathogens, this has subsequently decreased again and lupins play only a small role in the region. Faba beans *(Vicia faba)* and flax *(Linum usitatissimum)* are also occasionally cultivated, but neither has yet been widely adopted and it is not clear whether either will be (pers. obs). Studies on crop rotation in the region have so far indicated that it reduces crop disease pressure (Lamprecht et al 2011) and can result in higher overall farm profits (Basson 2017).

In addition to the gradual diversification of cropping systems, another major transformation of agricultural practices that has occurred in South Africa’s winter rainfall region in recent years is the adoption of conservation agriculture practices. These include minimised tillage and residue retention used alongside crop rotation (Kassam et al 2009), and it is estimated that around 80% of farmers in the region have now adopted these practices at least to some degree (Smit et al 2017). There are no statistics available for vineyards and orchards, but it appears that reduced tillage systems also dominate in these systems, although ‘minimum tillage’ actions that may include shallow soil disturbance with tools such as harrows and chisel ploughs are more common (pers. obs.). A greater proportion of arable farmers have switched to zero tillage (where the maximum soil disturbance is the use of a tine opener during planting). Some vineyard farmers also grow annual cover crops, which are terminated in spring and left to act as a mulch to protect the soil over summer. Overall, across both arable and perennial farming systems, minimising tillage and maximising crop residue retention have proven popular in the winter rainfall region as these practices can reduce soil erosion and surface crusting. They can also increase soil carbon content, which has productivity benefits through increasing soil moisture and nutrient retention (Bronick and Lal 2005, Swanepoel et al 2016, Smit et al 2017).

This history of increased crop diversification and conversion to conservation agriculture indicates that practices in the winter rainfall region’s commercial farming systems are shaped by the constraints of an arid climate and fragile soils, as well as by crop-specific difficulties, and the changing profit potential of various crops over time (Swanepoel et al 2016). Recent change in practices in commercial farms across South Africa appears to be primarily led by farmer ‘innovation platforms’, or networks of farmers set up to facilitate information sharing and on-farm trials (Smit et al 2017). These are integrated with government, agribusiness and academia through research foundations that receive funding through levies on grain sales. These distribute funding to research and extension activities deemed beneficial by their elected boards, who typically comprise a mixture of government officials, industry representatives, and farmers (e.g. PRF 2016). Thus, the conversion to conservation agriculture practices was primarily a farmer-led process, but with substantial support from these government-industry partnerships (Smit et al 2017). This is a shift from the apartheid era and earlier years, in which changes in practices appear to have been primarily top-down, being driven by the government through a mixture of regulations and subsidies (Meadows 2003).

Smallholder farming systems are rare in the winter rainfall region in comparison with other regions of South Africa, and perhaps due to this scarcity, it seems that little has been recorded about common smallholder practices. From a livelihoods perspective, ecological intensification is expected to be valuable to smallholders, as they are less able to afford inputs, and their low levels of access to resources, tools and information make them more vulnerable to market fluctuations and environmental perturbations than commercial farmers (Ncube, in press; Smith et al 2017). However, from the perspective of reducing agriculture's transgressions beyond the biophysical limits of the 'safe and just space for humanity', the obvious priority for research in South Africa's winter rainfall region are the large-scale, input-intensive, primarily white-owned commercial farms. Smallholders do not exist on such a scale to have such substantial impacts, and so the work in this thesis therefore focuses on large-scale, commercial farming systems. However, some of the practical studies may also be relevant to smallholder systems, given that they explore ecological principles and processes relevant to the region's climate and soils unique assemblage of farmed and non-farmed biodiversity. With a little further work, it would also be possible to use these to design ecological intensification practices appropriate to smallholder systems.

Agricultural sustainability and weed management in South Africa's winter rainfall region

The natural ecosystems of South Africa's winter rainfall region, part of the Cape Floristic Region, are recognised for their globally significant biodiversity and endemism (Cowling and Lombard 2002) and in 2004 were designated a World Heritage Site (UNESCO World Heritage Centre 2018). However, due to the economic importance of agriculture in the region, 26% of all natural habitat has been converted for agriculture (Rouget et al 2003), and critically, 93% of renosterveld, the region's dominant low elevation vegetation type of woodlands and scrub, has been lost (Kemper et al 1999). Natural vegetation is confined to a few less productive lowland pockets and to the steep slopes of the mountains. The result is a largely monotonous lowland landscape, with crop fields, vineyards and orchards interrupted only by the occasional alien tree (typically *Eucalyptus* or *Acacia* species from Australia) (see Figures 1.2-1.4).

This severe homogenisation of the landscape has not only caused extensive biodiversity loss but has also resulted in agricultural systems whose very simplicity makes them prone to degradation over time. The efforts to diversify arable cropping systems increased as wheat yields declined, but with only three or four crops available that can feasibly be regularly incorporated into rotations, relatively little headway has been made in enabling farmers to diversify their systems. This is a particular problem for weed management, as homogenised landscapes and simplified farming systems are known to promote the dominance of a few weed species that are well adapted to survival in the face of conventional management practices (Storkey et al 2010, José-María et al 2011, Garnier and Navas 2012). In both vineyards and arable systems of South Africa's winter rainfall region, *Lolium* spp. (hybrids of *L. rigidum, L. multiflorum* and *L. perenne;* Ferreira et al 2015) have become by far the most abundant, widespread and problematic weed (Pieterse 2010). Not only is *Lolium* very competitive in cropping systems, but is it also prone to developing herbicide resistance. Worldwide, *Lolium* species have evolved resistance to 11 herbicide sites of action (Heap 2014). In South Africa, tests have identified *Lolium* populations that are simultaneously resistant to up to three mode-of-action groups (Yu et al 2007, Pieterse 2010), whilst anecdotal evidence suggests there may be some populations in vineyards that are now resistant to all commercially available herbicides in South Africa.

In addition to the decreasing effectiveness of herbicides, there are other reasons to limit their use both in South Africa's winter rainfall region and around the world. Several herbicides are known to cause health problems amongst farm workers through frequent exposure (Mamane et al 2015) or can cause severe injury or death in the case of accidental spillage. It remains unclear whether exposure to herbicide residues through food poses a health risk (Benbrook and Landrigan 2015, Myers et al 2016). Some herbicides are also expected to reduce farm productivity, either through degrading soil microbe communities (Druille et al 2013), chelating minerals needed for crop nutrition (Mertens et al 2018), or through reducing the germination and growth in subsequent crops (Rose et al 2017). Herbicide drift can also impact susceptible crops on neighbouring fields: a recent case of drift in Australia resulted in damage to 5000 hectares of cotton *(Gossypium hirsutum)* crops (The Guardian 2017). Such drift events may also impact natural vegetation (Freemark and Boutin 1995, Prosser et al 2016), and herbicides can also leach into waterways where they may impact aquatic ecosystems (Relyea 2005, Annett et al 2014). Herbicides can also make their way into drinking water supplies, resulting in further risks to human health (Almberg et al 2018).

The primary alternative to herbicides for weed control is tillage, but given the observed benefits of minimum tillage practices in the Western Cape at reducing soil erosion and building soil carbon (Swanepoel et al 2015), reducing herbicides in favour of increasing tillage seems a dubious step to take in pursuit of agricultural sustainability. A more pragmatic approach is to accept that minimum and zero tillage practices make an effective contribution to sustainability in South Africa’s winter rainfall region due to the fragile soils and semi-arid climate (Meadows 2003, Giller et al 2015, Smit et al 2017), and to explore what other alternatives to herbicides apart from tillage could be used to further improve the sustainability of these systems. Weed management poses a challenge to conservation agriculture practices worldwide (Chauhan et al 2012, Bajwa 2014), and therefore addressing this need in South Africa’s winter rainfall region could also contribute to identifying processes and possibilities that may be globally relevant to improving weed management in minimum tillage systems.

Several alternative weed management practices to both herbicides and tillage are described in the literature. The most effective and widely applicable of these are generally considered to be crop rotation, as the basis of integrated weed management, the use of competitive crops to suppress weeds, and harvest weed seed management (Bajwa et al 2015, Nichols et al 2015, Liebmann et al 2016). However, none of these, either alone or in combination, seem able to replace both herbicides and tillage at present. Whether this is a question of the need to adapt more locally effective versions of these techniques, or whether additional techniques will always be needed to complement them, remains to be seen. Some tools, such as harvest weed seed destructors and robotic weeders, are prohibitively expensive to be realistic options for many farmers around the world, and particularly in South Africa given current exchange rates. Various other techniques, including biocontrol, allelopathy and crop nutrient management, are currently limited in their use by a lack of knowledge of which compounds and nutrients affect which weeds in which ways, and under which conditions (Bajwa et al 2015). The lack of knowledge on how such techniques can be implemented also makes it unclear how sustainable they would be in the long run, both in terms of their effects on agroecosystems and the surrounding environment, and the capacity of weeds to develop resistance. Therefore, whilst various possibilities for alternatives to tillage and herbicides exist, there is a need to explore both how these can be locally adapted and to consider their contributions to sustainability, before they could play a larger role in weed management.

In summary, the capacity of South Africa's winter rainfall region farming systems are limited in their ability both to meet human needs and to conserve natural ecosystems by the challenges presented by weeds in the context of current weed management options. In order to make progress toward farming systems that are able to stay within the 'safe and just space for humanity', new options for weed management in the region are required that:

a) are effective against herbicide-resistant weeds;
b) do not require intensive herbicide use or soil disturbance;
c) can be achieved with available and economically feasible crop species and tools;
d) contribute to restoring natural biodiversity and ecosystem functioning.

This thesis presents the first investigation of ecological intensification as an approach to meet the specific needs of sustainable weed management in South Africa's winter rainfall region. Ecological intensification is considered a promising approach to do this due to its inherent and explicit consideration of the long-term interactions between weeds, farm management, the agroecosystem, and the surrounding environment. Furthermore, ecological intensification can be expected to contribute to the wellbeing of farmers and rural communities through providing them with approaches that reduce their dependence on input markets and provide more freedom to manage their lands in a way that avoids health risks and environmental degradation whilst sustaining production and incomes.

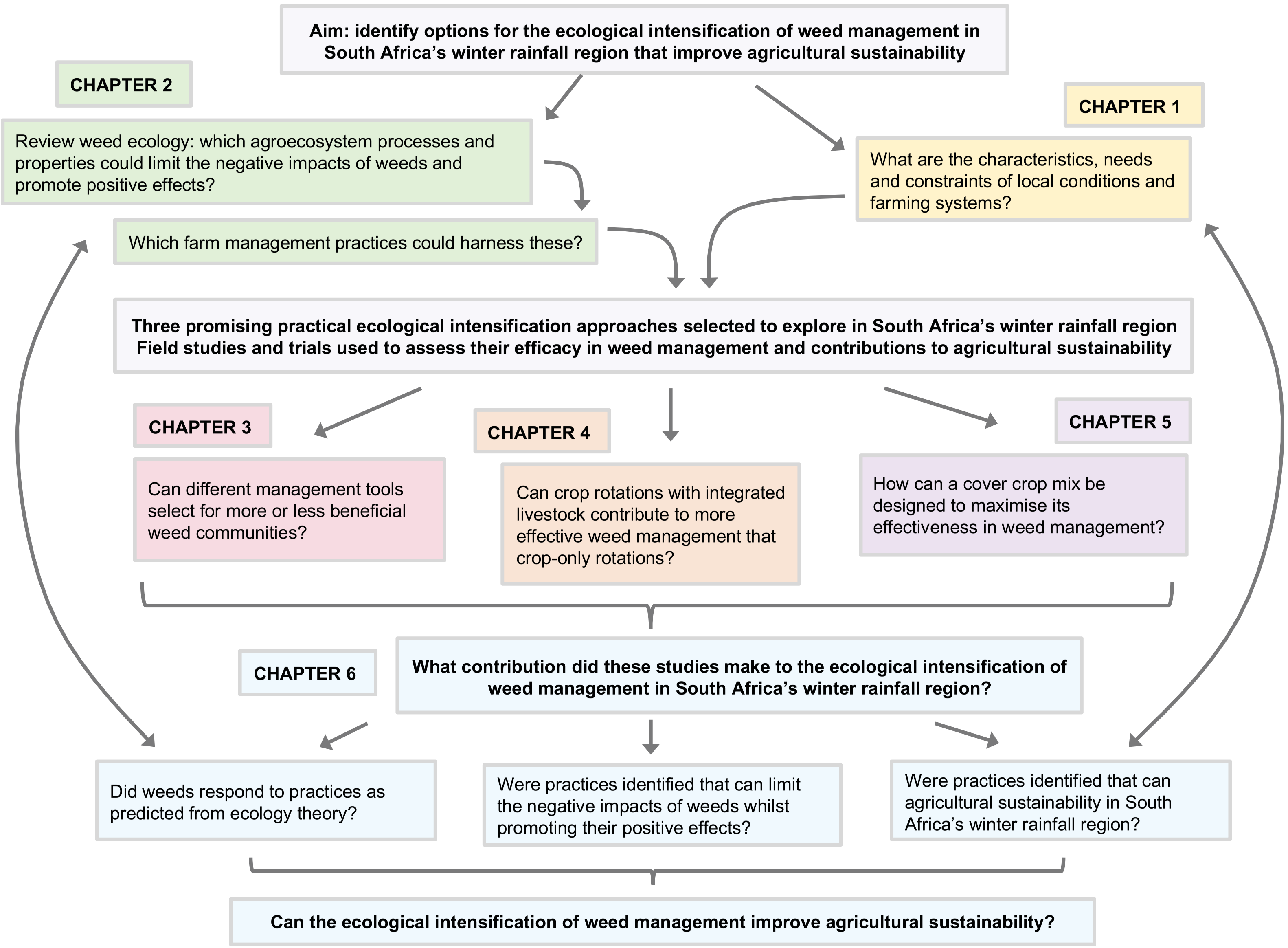
1.4 Thesis aims, objectives and structure

The overarching aim of this thesis is to identify options for the ecological intensification of weed management in South Africa's winter rainfall region that can improve agricultural sustainability in the face of the region's specific weed challenges, and in the context of the region's farming systems and local conditions. The thesis addresses this aim following the process outlined in Figure 1.5. It begins by drawing together general theories in ecology with relevance to weed management, then combines these with existing research in weed management to identify promising practical approaches for ecological intensification (Chapter 2). Three specific practical approaches that are appropriate to South Africa's winter rainfall region are then explored through a series of field studies and experiments (Chapters 3 – 5). The review chapter and three practical chapters are presented as investigations into weed management underpinned by ecological theory, with global implications for weed management as well as practical outcomes for South Africa's winter rainfall region. Each is presented as a stand-alone scientific article as each makes an individual contribution to advancing knowledge of weed management.

The topics addressed in each practical chapter are all linked by ecological theories identified in the review (Chapter 2), and all were chosen through discussion with local researchers engaged with regional farmers' networks, so that topics considered current priorities by farmers and local researchers could be selected (although the choice was also constrained by time, logistics and budget considerations). Choosing current priorities was intended to maximise the potential adoption of any useful findings by farmers as well as opportunities for collaboration with local researchers. Collaboration was considered important to ensure that studies and experiments undertaken were relevant in the local context and that any findings could be appropriately disseminated through local networks. Also in the interests of facilitating adoption of any positive findings, each practical weed management option explored in the practical chapters was also assessed in the context of whether it contributed to sustaining yields and/or profits. Understandably, farmers may not be willing to adopt practices that result in yield or profit penalties, although it has been shown that avoiding health risks and contributing to nature are sometimes considered worth a certain reduction in income (Mzoughi 2011, Hamann et al 2015).

Following the ecological intensification approach, each practical chapter uses ecological theory to inform a specific question about weed management. This allows for weed management studies or trials to both answer applied management questions ('does this work and how?') as

Figure 1.5: A schematic of the approach taken by this thesis to address its overarching aim, with the content of different chapters coded in different colours.



well as to test relevant aspects of ecological theory (‘do the weeds behave as theory predicts?’). Therefore, in addition to the overarching aim of this thesis presented above, each chapter also had a specific objective relating to the application of ecological theory to weed management. These objectives are presented at the end of Chapter 2, as they are based on theories identified in the review of weed ecology and thus require Chapter 2 to provide their rationale and context. Each ecological objective is also presented as testable hypotheses in the introduction sections of each of the Chapters 3 – 5.

All chapters of this thesis contribute to addressing the overall knowledge gap of identifying ecological intensification strategies that have potential to improve the sustainability of weed management in South Africa’s winter rainfall region. Each practical study makes additional individual novel contributions to weed ecology theory. Chapter 3 presents the first application of functional trait and ecological filter theory to agricultural weeds in South Africa. Chapters 4 and 5 are novel globally: Chapter 4 presents the first long-term analysis of weed trends in integrated crop-livestock rotation systems, while Chapter 5 is the first trial to systematically explore the effects of cover crop composition, species diversity and functional diversity on weed suppression.

Given the dual aim of each chapter to identify practical options for sustainable weed management and to advance knowledge of weed ecology, the discussion chapter evaluates each chapter from both perspectives. It concludes by discussing what the overall findings of this thesis suggest about the value of ecological intensification for weed science, weed management and agricultural sustainability in general, and for South Africa’s winter rainfall region in particular.

1.5 A note on thesis format and author contributions

This thesis is presented in article-based format, with Chapters 2-5 (the literature review and three practical case studies) written in the style of academic publications. This introduction and the discussion serve the purpose of tying those chapters into a cohesive narrative that explains their overall contribution to knowledge. In keeping with this format, references cited are included at the end of each chapter.

At the date of submission of this thesis, Chapter 4 was published in the *Journal of Applied Ecology* (MacLaren et al 2018), and Chapters 3 and 5 were under peer review. Each of these chapters was completed in collaboration with supervisors and researchers from other institutes. In all cases the research questions and hypotheses were posed by the author of this thesis, and the vast majority of fieldwork, data analysis and writing was also conducted by the author as outlined here:

Chapter 3: The author posed the idea for the study and devised the experimental design with input from her supervisors (Katharina Dehnen-Schmutz and James Bennett). All field work, including identifying suitable farms, undertaking weed surveys and management questionnaires, and collecting soil samples, was conducted solely by the author. Soil samples were analysed by Stellenbosch University laboratory staff. The author completed the data analysis independently and a first version of the article independently, and collaborators provided suggestions on content and style that led to an improved final version.

Chapter 4: This chapter is based on long-term data collected as part of a larger long-term (20 year) agronomic trial, the Langgewens Long-Term Crop Rotation Trial (described in Hardy et al 2011) which is currently managed by Johann Strauss of the Western Cape Department of Agriculture. This trial is set up to collect agronomic measures of different rotation systems, and the author recognised the opportunity to use the weed data from this trial to compare the effects of crop rotation, management diversity and livestock integration in a novel way. All collaborators (Jonathan Storkey, Pieter Swanepoel, Johann Strauss and Katharina Dehnen-Schmutz) contributed to discussions on how best to approach this, but the final hypotheses and direction of the study were determined by the author. The author also extracted the relevant data from the overall trial dataset, decided on the analysis procedures, and produced a first draft of the article (which was refined with contributions from the collaborators). Using a long-term dataset is necessary to understand the effects of temporal diversity in farming systems, given that a number of years must pass before the overall effect of differences between years can be observed. In the timeframe of a PhD it would not have been possible to collect sufficient data, and so the Langgewens Trial dataset presented a valuable opportunity to explore the potential of crop rotation in ecological intensification.

Chapter 5: Based on the theories discussed in the literature review (Chapter 2), the author developed the conceptual framework for the trial to compare the roles of species diversity, functional diversity and composition of cover crops in weed suppression. She received advice on species selection, experimental design and data collection from collaborators, and benefited in her interpretation of the data from discussions on plant-soil interactions, soil nutrient cycles, and local soil conditions with collaborators. However, the author made the final decisions on study design, and conducted the fieldwork and data collection, sometimes with assistance from local technicians and field assistants. The author undertook all the analysis and writing, with collaborators providing critical revisions of the analysis and article.

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CHAPTER 2: ECOLOGICAL STRATEGIES FOR INCREASING AGROECOSYSTEM RESILIENCE TO WEEDS - A REVIEW

2.1 Abstract

Re-framing the goal of weed management to ‘agroecosystem resilience to weeds’ could overcome the problems of environmental damage and resistant weeds associated with conventional weed management. ‘Resilient agroecosystems’ would be designed to incorporate properties and processes that inherently limit the negative impacts of weeds without requiring substantial weed control actions, and also to sustain sufficient weeds to support farmland biodiversity and contribute to soil quality. To understand how this could be achieved, this review draws together recent advances in weed ecology to identify processes that would underpin agroecosystem resilience, then explores practical opportunities to integrate these processes into agroecosystems. Overall, practices that increase diversity in management, resources, biota and landscape composition facilitate processes that confer resilience to the negative impacts of weeds. Maintaining appropriate levels of disturbance and resource availability would also select for weed communities that are expected to be less competitive with crops. Several well-established practices, such as crop rotation, intercropping and integrated crop-livestock systems, can be used to increase diversity and to moderate disturbance and resource levels, and thus increasing the adoption of such practices around the world would advance the sustainability of weed management. New developments such as breeding cooperative and perennial field crops may further enhance capacity to create agroecosystems that are resilience to weeds.

2.2 Introduction

Balancing agricultural production with environmental conservation is a critical challenge of our times. The human population continues to grow while global biodiversity declines at unprecedented rates (Ceballos et al 2015), threatening the integrity of the world’s ecosystems and their capacity to provide life-supporting services to sustain humanity (Foley et al 2005, Newbold et al 2016). Agriculture is a major cause of biodiversity loss and decline in ecosystem services, through habitat conversion, pollution, and carbon emissions (Stoate et al 2001, Tilman et al 2002). Increasing agricultural intensification in recent decades has resulted in an unprecedented decline in farmland biodiversity, and further increased the impacts of agriculture on off-farm ecosystems (Geiger et al 2010, Baudron and Giller 2014).

Weed management is key to whether agriculture conserves or undermines biodiversity and ecosystem functioning, both on-farm and off-farm (Freemark and Boutin 1995, Lal 2004). Weeds are removed from agricultural land to prevent them from competing with crops and pastures, and it has been estimated that weeds could reduce global yields of major crops by up to 34% if not controlled (Oerke 2006). However, it is becoming increasingly apparent that the conventional focus of weed control on maximising weed removal is unsustainable. Intensive weed control is linked to a loss of plant diversity on farms (Storkey et al 2010, 2012) and a loss of abundance and diversity in farmland insects, birds and small mammals (Freemark and Boutin 1995, Marshall et al 2003). Keeping soil clear of the vegetative cover provided by weeds can also lead to soil erosion and the loss of soil organic matter (Lal 2015, Blaix et al 2018), reducing the capacity of soil to retain water and nutrients and to sustain microbial functions. Soil erosion and degradation also result in off-farm impacts such as carbon emissions and the siltation of waterways (Pimentel et al 1995). These impacts on soil are worsened by the regular soil disturbance of intensive tillage (van Oost et al 2006), and herbicides may also pollute waterways (Annett et al 2014) and cause damage to natural vegetation and to crops (Freemark and Boutin 1995, Martinez et al 2018). Herbicides can also pose health risks to people, both farmworkers and consumers (Mamane et al 2015, Myers et al 2016).

Furthermore, the reliance of conventional farming systems on herbicides and tillage has decreased the effectiveness of these practices for weed control over time, as weed species have adapted to these control measures and tolerant species have increased in abundance (Johnson et al 2009). Conventional agricultural landscapes now tend to be dominated by a few weed species that are difficult to control by these means (Neve et al 2009, Garnier and Navas 2012), and the ability to resist herbicides has evolved independently in multiple populations of multiple weed species (Mortensen et al 2012). The substantial energy expended and environmental costs incurred in attempting to manage these weeds no longer necessarily results in successful weed control nor in higher crop yields (Gaba et al 2016).

A range of alternative weed control techniques alongside tillage and herbicides exist (Bajwa et al 2015). However, it seems impossible for any single technique to prove a panacea for weed management, given the ubiquity, diversity, plasticity and adaptability of weeds around the world. The recent introduction of harvest weed-seed destructors and collectors was heralded as a potential method to control herbicide-resistant weeds (Walsh et al 2013), but there is already documented evidence that certain species are adapting to this technology through earlier seed shedding, thus avoiding harvest seed destruction (Ashworth et al 2015).

The adaptability of weeds means that the harder we try to remove weeds, the harder they become to remove. Expending more effort to control weeds also increases the damage done to agroecosystems and the surrounding environment (Smith 2015). Previous research suggests that the most effective and sustainable forms of weed management are those that shift the focus away from killing weeds to creating conditions that are less favourable to weeds, so that less weed control is required (Anderson 2005, Chauhan et al 2012, Davis et al 2012). This has been best achieved in rotation-based farming systems that follow an ‘integrated weed management’ (IWM) approach, incorporating a variety of different weed control actions and cultural management techniques (Swanton and Weise 1991). Such an approach varies the conditions experienced by weeds each year, and uses ‘many little hammers’ (Liebmann and Gallandt 1997) to limit weed growth or reproduction in multiple ways at multiple points in their life cycles (Sanyal et al 2008). This reduces the chances that any species will encounter favourable conditions for population expansion each year, and also reduces selection pressure for adaptation to specific management actions. There is evidence that such approaches can sustain farm profitability at reduced levels of environmental impact (Davis et al 2012).

There are some current limitations to how IWM strategies are implemented, given that most simply aim to avoid herbicide resistance whilst still removing as many weeds as possible, with no explicit consideration of the relationships between weeds, the agroecosystem, and the wider environment. Harker & O'Donovan (2013) and Owen et al (2015) comment that in many cases IWM has simply become 'integrated herbicide management', where the only variation in weed management consists of different herbicide mode-of-action groups used in different years. It is still possible for resistance to multiple herbicides to evolve in these systems, or for species with pre-existing multiple resistance to colonise them (Mortensen et al 2009, Owen et al 2015). Much of weed science has become fixated on the physiological mechanisms through which herbicide resistance develops (Neve et al 2009), whilst less attention is paid to integrating our increasing knowledge of broader weed biology into new, more systems-focused approaches to management (Ward et al 2014, Neve et al 2018). This is at odds with the fundamental reason that well-implemented rotation-based IWM strategies remain the most successful weed management strategy in the long term (Bàrberi 2002, Chauhan et al 2012, Owen et al 2015): that the process of natural selection drives plants to specialise to specific conditions, and so by varying the conditions experienced by weeds, this process can be manipulated to limit weed population growth. The success of this approach indicates that further advances in weed science could be achieved by investigating other ecological processes determining weed populations and communities, so that it becomes possible to design agricultural systems that direct these processes toward favourable outcomes for both agricultural productivity and environmental conservation.

In general, farming systems that are designed to fit into and take advantage of ecological processes have greater potential to sustain long-term productivity and to limit damage to biodiversity and ecosystem functioning (Ewel 1999, Tittonell 2014, Weiner 2017). In recent years our knowledge of weed ecology and plant ecology in general has advanced substantially, revealing new opportunities for weed management that could contribute to sustainable and restorative farming systems. The aim of this review is to synthesise these advances, to identify the most promising opportunities to translate ecological theory into practical strategies that can be implemented by farmers, and to highlight new directions for weed research. To achieve this, we begin by considering ‘resilience to weeds’ as a paradigm to underpin more effective weed management based on ecological processes. We then investigate what current knowledge in weed ecology suggests that ‘resilience to weeds’ would look like in terms of ecosystem processes, then explore practical approaches that can introduce or enhance these processes in agroecosystems. Lastly, we reflect on implications of this approach for future weed management and weed research.

2.3 ‘Resilience’ to weeds

To maximise the sustainability of weed management from both environmental and economic perspectives, it is first critical to shift the focus of weed management away from the weeds themselves and instead to designing farming systems that take weeds into account. This creates opportunities to optimise the whole system in a way that takes balances both the negative and positive impacts of weeds with other costs and gains involved in agricultural production (Bàrberi 2002, Petit et al 2011, Colbach et al 2014a). Such an approach prevents weed management being added to farming systems as an expensive and environmentally damaging afterthought. We propose that this can be more easily achieved if weed research aims to improve agroecosystem ‘resilience to weeds’ rather than ‘weed management’.

The word ‘resilience’ was first adopted in an ecological context by Holling (1973), who defined ecological resilience as a “the persistence of systems and their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables”. Resilience has since become a widely used term in ecology and other disciplines, often in ways that differ somewhat from Holling’s original definition. However, most definitions of resilience involve the *response* of a system or an individual to a *disturbance*, producing a desired *outcome* (Döring et al, 2015). In the context of weeds, the desired outcome is that agroecosystems can sustain production of food, fuel and fibre whilst providing farmers with decent livelihoods and avoiding negative impacts on the surrounding environment. Acknowledging that weeds can have both positive and negative effects on production (Petit et al 2011, Gibson et al 2017, Blaix et al 2018), and that it is economically and environmentally desirable to minimise weed control actions (Clements et al 1995, Lal 2004), a resilient response to weeds would thus entail an agroecosystem’s capacity to sustain production *despite* the presence of weeds. Therefore, the resilience is to the negative effects of weeds, not the to the presence of weeds themselves. Depending on one’s definition of the word ‘weed’, it could be re-phrased that agroecosystems should be resilient to ‘weeds’ but capable of conserving ‘wild plant diversity’ (see Zimdahl 2013 for a discussion on definitions).

A key characteristic of resilient systems is the capacity to self-regulate; that is, that they can resist, recover from or adapt to adverse events without external interference (Fischer et al 2006, Cabell and Oelofse 2012, Döring et al 2015). In terms of weed management, this implies the design of agroecosystems that do not require farmers to implement energy intensive or resource intensive measures specifically aimed at weed control. Instead, the agroecosystem should incorporate processes that naturally limit weeds’ negative impacts and promote their positive effects. A simple example of this would be crop rotation, which is incorporated into agroecosystems due to its multiple benefits for productivity and sustainability, and which also limits weed population growth by changing the conditions experienced by weeds each year.

An ecological intensification approach can be used to understand how agroecosystems could self-regulate their weed communities. Under ecological intensification, improvements to agricultural productivity and sustainability are sought by identifying the processes of natural ecosystems that allow them to sustain certain structures and functions (Tittonell 2014). Processes that confer desirable functions for agriculture, such limiting weeds’ negative effects and promoting their positive ones, can then be mimicked in agroecosystems (Ewel 1999, Doré et al 2011). Such an approach has the advantage of working with ecology rather than against it, and can thus avoid situations such as the evolution of herbicide resistance, where it is difficult to prevent ecological processes from keeping weeds one step ahead of weed management. Using ecological intensification to create agroecosystems that are resilient to weeds therefore has high potential to enable truly sustainable weed management.

The main negative effects of weeds are competition with crops, allelopathy and their potential to host crop pests and pathogens (Zimdahl 2013, Håkansson 2003). All these effects increase as weed abundance increases, and increase proportionally more if the proportion of particularly competitive, allelopathic, or pest-supporting weed species increases. The positive effects of weeds, such as soil protection and provision of resources to higher biodiversity, can also increase as weed abundance increases and as the proportion of weeds that perform these functions to a greater degree increases. These are also more likely to increase as the diversity of weeds increases (Díaz and Cabido 2001, Isbell et al 2011). Therefore, we are concerned with both the *quantity* of weeds as well as their *quality,* the composition and the diversity of the weed community. Resilience to weeds implies that an agroecosystem is able to maintain a stable state in which the weed community is sufficiently low in quantity to avoid negative impacts, but sufficiently high in both quantity and quality to perform positive functions.

2.4 The ecology of weed quantity

The quantity of weeds, in terms of biomass, abundance and density, has been the traditional focus of both weed science and weed management (Håkannson 2003, Zimdahl 2013). Crop yield decreases as weed quantity increases, primarily due to competition between weeds and crops (Zimdahl 2007), and thus it is essential that farmers have tools and approaches available to limit weed quantity (Oerke 2006). However, it is important to note that the relationship between weed quantity and crop yield is not constant under different conditions (Ryan et al 2009, Swanton et al 2015), and also that the optimal weed quantity may not be the lowest possible, if the costs of weed control and the benefits of weeds are taken into account (Clements et al 1995, Petit et al 2015).

Trends in weed quantity have traditionally been explored via the field of population ecology, the study of the processes that drive the abundance and distributions of different species. Essentially, a population of weeds increases when immigration, reproduction and recruitment outweigh mortality and emigration. To understand when and how this occurs, weed population ecology is concerned with weed seedbank dynamics, seedling establishment, weed growth, and seed or propagule production (Figure 2.1; Davis 2017). The rate at which these dynamics occur, and whether or not weeds survive their transition from seed to seed-producer, are influenced by farm management, the local environment, and interactions with crops, livestock, and other weeds and unfarmed biodiversity (Mortensen et al 2000, Chauhan et al 2012). Therefore, to understand weed population dynamics, it is important to understand how the different elements of agroecosystems can either facilitate or limit weed survival and reproduction.

Studies of alien plant invasions in natural ecosystems shed some light on agroecosystem vulnerability to weeds, revealing that fluctuating resource levels and low biotic resistance are two key characteristics of ecosystems that determine how easily arriving plants can invade (Richardson and Pyŝek 2006, Catford et al 2009, Jeschke 2014). Fluctuating resource levels occur when regular disturbance releases resources (light, water and nutrients) from capture by extant biomass, and regular disturbance thus creates repeated opportunities for newly arriving species to exploit these resources to establish (Davis et al 2000). In agroecosystems, regular harvesting and weed control actions release resources from crops and existing weeds, which are then available to new weeds, whether they are already present in the soil seedbank or arrive via dispersal from elsewhere. As discussed by Smith (2015), such management actions keep annual agroecosystems in a permanent state of early succession, where the underlying ecological process is simple: if resources are available, weeds will make use of them to establish.

Weeds also typically do not face strong biotic resistance to their establishment in agroecosystems. Biotic resistance can be defined as the ability of a resident ecosystem to prevent new species from establishing and spreading via biotic interactions, such as competition or herbivory (Levine and D’Antonio 1999, Richardon and Pyŝek 2006). There are few opportunities for this to occur in conventional agroecosystems, where habitat simplification and pesticide use ensures that weeds face few herbivores or seed predators (Navntoft et al 2009), and where monocultural crops may be relatively inefficient at competing for resources compared with a diverse plant community (Funk et al 2008, Finn et al 2013).

The lack of biotic resistance and the abundance of resources leaves weed control actions as the main mechanism to limit weed survival in agroecosystems (Figure 2.1). This increases selection pressure for weeds to adapt to control, by removing the fitness costs to weeds if adaptations to control also increase vulnerability to herbivory or stress. The consistent use of the same control techniques further increases selection pressure for adaptation, given that it is relatively easy to possess or evolve traits conferring tolerance to one type of control compared with several traits to tolerate multiple adverse events or conditions (Neve et al 2009). The classic illustration of the effect of simplified farming systems on weeds is the spread of herbicide resistance, where herbicide-dominated weed control strategies allow weeds possessing resistance genes to escape control entirely, and thus within a few years, a few individual weeds possessing resistance genes can lead to resistant weed populations that threaten productivity across entire agricultural regions (Powles 2007, Mortensen et al 2012). Re-integrating natural enemies, resource limitations and variable weed control actions into agroecosystems could therefore limit weed population growth by diversifying the selection pressures faced by weeds.

Models that simulate the population dynamics of problematic weed species also tend to conclude that tactics that limit weed survival in multiple ways, for example by targeting weeds at multiple points in their life cycle, are more effective at limiting weed quantity than single control actions (e.g. Tidemann et al 2016, Andrew and Storkey 2017). These types of models can be useful to identify how best to integrate diverse tactics to manage problematic weeds. However, they are often limited to the site, conditions and species for which they were parameterised (Mortensen et al 2000, Holst et al 2007). Recent progress in assembling databases of plant traits and population parameters for a greater number of species has begun to overcome these limitations,

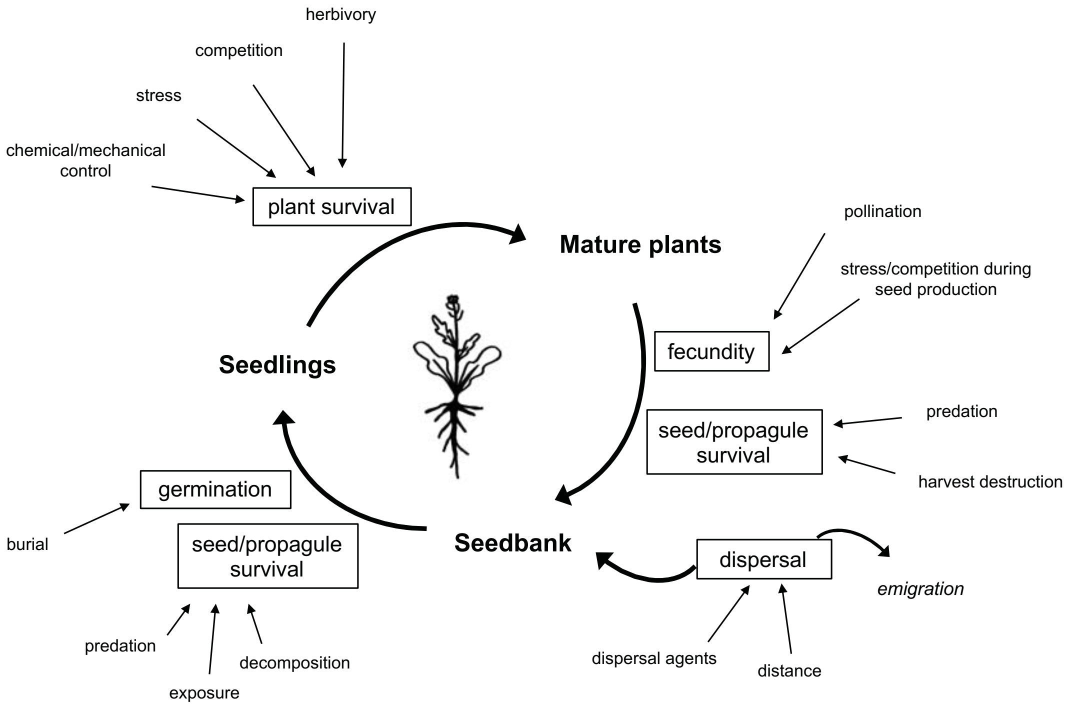

Figure 2.1: A simplified weed life-cycle showing the life stages (bold text) and the processes that occur as weeds move from one life stage to another (text boxes). Events or pressures that may increase, moderate or interrupt these transitions are also indicated (small text).

and permit the development of models that can incorporate multiple species as well as greater environmental and management variation, and that can even take the potential benefits of weeds into account (Colbach et al 2014a, Mézière et al 2015). Thus, models of weed populations are developing into models of weed communities, and their power to explore and predict the effects of different cropping systems and management decisions on both weed quantity and quality is increasing. A key element of understanding how to manage populations of different weeds simultaneously is thus to understand how and why different weeds interact in different ways with weed management and with other elements of agroecosystems. To address this, the next section explores the determinants of weed community composition and weed diversity, and how these can affect both crop production and environmental conservation.

2.5 The ecology of weed quality

The composition and diversity of a weed community can be considered ‘quality’ in that differences between weed species determine their relative abilities to compete with crops, support biodiversity and perform other ecosystem functions. Community composition and diversity are determined by community assembly processes (Booth and Swanton 2002), in which the set of traits possessed by each weed species determines whether it is capable of dispersing to a site, and of surviving the local environmental conditions and biotic interactions encountered at that site (Figure 2.2). Barriers to dispersal and survival act to filter the species that can persist in a community, by removing those species that lack the requisite traits to pass the barriers (Kraft et al 2015). Strong filters therefore lead to low diversity communities whilst weaker filters allow for more diverse communities. Community assembly theory was first applied to weed management by Booth and Swanton (2002) who proposed it as a framework to understand how agroecosystem management, environmental conditions and biota determine the weed community, and to infer how and why weed communities change over time. Since then, numerous studies have investigated how different landscape and field management practices select for different types of weeds and different levels of weed diversity (e.g. Gabriel et al 2005, Ryan et al 2010, Storkey et al 2010, José-María et al 2010 and 2011).

These observed differences in weed community composition in response to farm management raised the question of whether different weed communities result in different effects on the agroecosystem. To answer this, the ‘response-effect’ functional trait framework (Lavorel and Garnier 2002, Suding et al 2008) has been integrated into weed community assembly studies (Navas 2012, Gaba et al 2017). A functional trait can be defined as a morphologicial, physiological or phenological trait that affects an individual organism’s fitness (Violle et al 2007), and the ‘response-effect’ trait framework posits that traits determining an organism’s response to its conditions will also determine the effect of that organism on its environment. Thus, one can infer from weed traits how the ecosystem functions performed by a weed community will change in response to management or environmental conditions (Lavorel and Garnier 2002, Garnier and

Figure 2.2: Community assembly theory applied to weeds (modified from Booth and Swanton 2002). The shading of the bars represents filter strength, and the arrows widths indicate that more species are able to pass through weaker filters.

Navas 2012). The ‘response-effect’ framework can be used to make generalisations about the effect of agricultural management practices on weeds and their functions due to the inherent dimensionality between plant traits (Laughlin 2014, Reich 2014, Díaz et al 2015). This dimensionality results from certain groups of traits conferring adaptation to certain conditions and resulting in certain ecosystem functions, and thus species that share these groups of traits can be grouped into ‘functional types’.

Life history strategy can be an informative approach to grouping weeds by shared functional traits, given that life history strategies vary in response to disturbance intensity and resource availability (Grime 1977, Westoby 1998, Bohn et al 2014), and both of these are strongly influenced by farm management in agroecosystems (Gaba et al 2014). To the extent of current knowledge, two key dimensions appear to describe the majority of plant life history variation worldwide (Adler et al 2014, Díaz et al 2015; Figure 2.3). The first of these is the ‘fast-slow’ economics spectrum (a whole-plant extension leaf economics spectrum; Reich 2014). ‘Fast’ plants are capable of rapid resource uptake and turnover but require high resource availability to sustain their physiology, whilst ‘slow’ plants can tolerate stress through resource conservation and recycling, but these mechanisms limit the rate at which they can capture resources (Adler et al 2014, Reich 2014). The second dimension is the ‘r/K selection’ dimension (MacArthur and Wilson 1967), with r-selected plants producing many small seeds that need a favourable environment for successful establishment, whilst K-selected plants produce fewer large seeds that are more capable of tolerating stress or competition (Moles and Westoby 2006). These two dimensions are related to Grime’s (1977) ‘ruderal/competitive/stress-tolerant’ life history triangle, with ruderal species tending to be *r*-selected and competitive species *K*-selected, whilst stress-tolerant species have a ‘slow’ physiology (Figure 2.3). On the global spectrum of plant strategies, weeds tend to follow ‘ruderal’, ‘fast’ or ‘r-selected’ life strategies in response to the high disturbance frequencies and high resource availabilities that distinguish agroecosystems from natural ecosystems (Baker 1974, Smith 2015). As agricultural intensity increases, in terms of increasing disturbance, resource availability and landscape simplification, selection for ‘faster’ physiologies and ‘r’ reproduction strategies becomes more intense (Garnier and Navas 2012). Larger-seeded weeds with ‘slower’ life strategies tend to be lost from intensive agriculture (Storkey et al 2010, Storkey et al 2012, José-María et al 2011).

Agroecosystems that select for such traits may increase weed competition with crops, given that ‘fast’ life strategies confer competitiveness through rapid resource capture, which reduces resource availability to their neighbours (Reich 2014, Swanton et al 2015). This would be particularly true in annual systems where annual harvest, weed control and crop sowing resets the ‘race’ for resources between crops and weeds each season. In contrast, the least competitive weeds are expected to be species with a ‘slow’ and ‘stress-tolerant’ life strategy. These species would be less competitive with crops due to slower rates of resource uptake, but also more

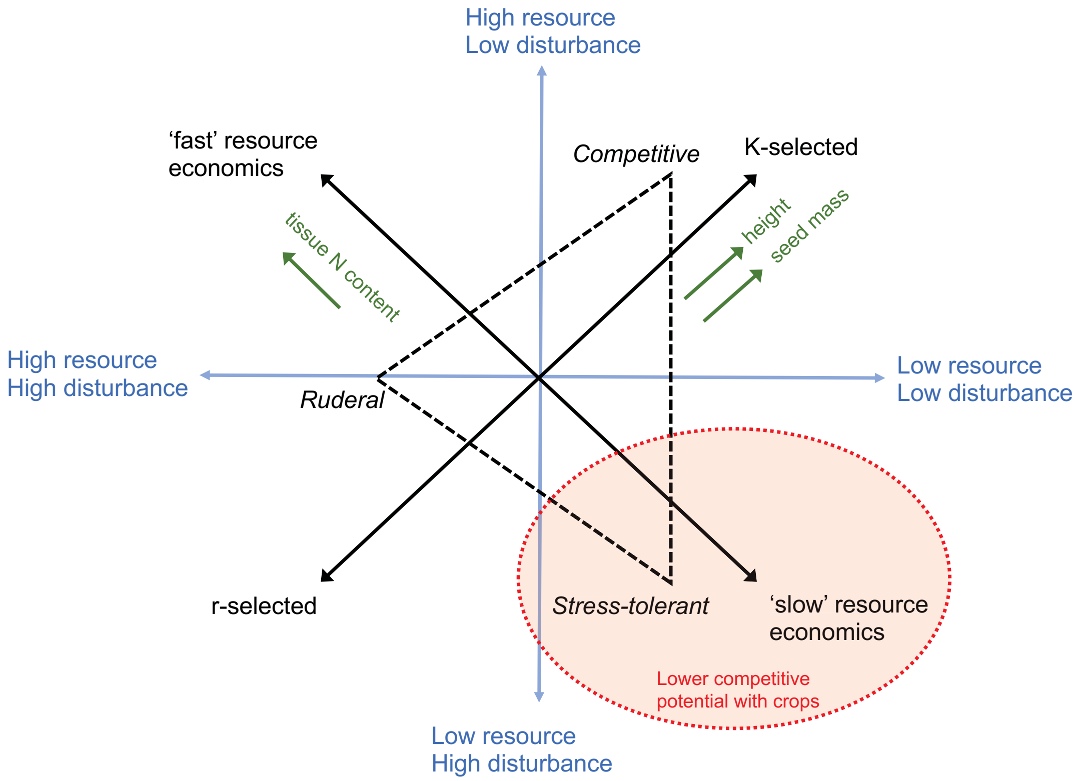

Figure 2.3: Schematic showing how different disturbance levels and resource availability are expected to select for weeds with different life history strategies, based on several existing theoretical frameworks including Grime's (1977) "CSR" life history triangle, MacArthur and Wilson's (1967) *r-/K*-selection reproduction spectrum, and Reich's (2014) 'fast-slow' economic strategy spectrum. Evidence of trait dimensionality presented by Westoby (1998) and Díaz et al (2015) suggests that synthesising these theoretical frameworks in this way explains much observed variation in global plant life history strategy in response to disturbance and resource availability.

tolerant of the stress imposed by competition from crops (Andrew et al 2015, Poorter et al 2015), and so more able to persist amongst crops to support biodiversity. Weeds with such life strategies would be expected to occur more under conditions of low resource availability and an intermediate level of disturbance (Figure 2.3). In contrast, low disturbance would start to select for species that are more competitive over the long term, such as perennial woody weeds, and an increase in such species has been observed when tillage disturbance is reduced in organic farming systems (Armengot et al 2015, Halde et al 2015). Meanwhile, high disturbance rates would promote species that are both 'faster' and more 'ruderal' (Figure 2.3).

Another strategy to promote weed species with specific life history strategies in agroecosystems may be the management of non-cropped areas. For example, farmers who spray their fencelines or headlands to avoid these becoming ‘reservoirs of weeds’ are consistently creating environments where only weeds adapted to establishing in bare soil and growing rapidly between spray events, or tolerating spray events, could survive. These may then act as a seed source of ‘fast’ *r*-selected weed species that would impose high early-season competition on annual crops. In contrast, fencelines and headlands planted with perennial species (trees, hedges, or grass and wildflower mixes) would be more likely to select for slower, shade-tolerant weed species. Increasing the habitat diversity at a farm or landscape level is also expected to promote the natural enemies of both weeds and crop pests (Gurr et al 2003, Trichard et al 2013).

It is unclear how life history strategy traits influence the value of weeds to biodiversity. Selecting for ‘slow’ species may increase the quantity of weeds that could co-exist with crops, but may reduce the value of each weed biomass unit to herbivores, as ‘slow’ species typically have a lower nitrogen content per unit mass (Reich 2014, Díaz et al 2015). Various other weed life history traits including seed size and seed energy content are also important to biodiversity, but such relationships are only just beginning to be explored and strong trends are not yet clear (Gaba et al 2017). Other traits less related to life history strategy can also be important for biodiversity (e.g. flower attractiveness, nectar quality, and mycorrhizal associations for pollinators; Gaba et al 2017) but it is not clear how traits not related to life history strategy respond to agricultural intensification.

A different approach to reduce the competitiveness of weeds with crops would be to select for weeds that use resources in ways that are divergent from and complementary to those of crops. The principle of limiting similarity suggests that the use of competitive crops should impose selection pressure on weeds to diverge from crops in resource use patterns (MacArthur and Levins 1967); however, studies indicate that environmental filtering in agroecosystems is instead sufficiently strong to select for weeds that mimic crops (Garnier and Navas 2012). Conditions created to favour crops also favour weeds with the same phenology and nutrient demands as crops (Fried et al 2009). It is possible that increasing the diversity of resource types within a farming system would promote weeds adapted to use different resources from the crop (‘the resource pool diversity hypothesis’; Smith et al 2010). For example, simplified cropping systems reliant on inorganic fertilisers to provide nitrogen would select for weeds able to compete with crops for that particular nitrogen source, whereas systems incorporating legumes or manures may provide more opportunities to weeds to specialise to use different forms of nitrogen (Smith et al 2010).

Diverse crop rotations associated with management variation would also be expected to reduce selection for crop mimics by selecting for different weed species each year, so that the overall weed community does not come to be dominated by weed species that mimic any particular crop. Increasing weed diversity may therefore be important to reduce weed competition with crops, in addition to selecting for less competitive functional types. Increased weed diversity is also expected to support higher diversity at other trophic levels (Marshall et al 2003), and to result in a greater provision of a greater diversity of ecosystem functions (Isbell et al 2011). Weed diversity can be promoted through both ‘top-down’ management, in terms of varying the management-induced filters and biotic interactions experienced by weeds, through landscape management, the choice of weed control actions and crop rotation. ‘Bottom-up’ management may also increase weed diversity, given that diversifying the nutrient sources available to weeds would facilitate the co-existence of species adapted to different nutrient sources (Smith et al 2010).

In some systems, it may be possible to tailor weed management choices to promote divergence in resource use between weeds and crops. For example, in perennial cropping systems such as vineyards and orchards, tall weeds (which also tend to be deeper-rooted; Garnier and Navas 2012) may impose greater competition with the crop due to an increased overlap in rooting depth and leaf canopy. The use of a management technique such as mowing that directly selects against tall species may thus shift the weed community to one that is inherently less competitive with the crop.

To summarise this section, weed community composition and diversity can influence the potential competitiveness of a given quantity of weeds, and their potential to support biodiversity and perform other ecosystem functions. Intensive agriculture, in terms of increased disturbance, increased resource availability and increased landscape simplification, creates selection pressure for a low diversity of ‘fast’ r-selected species that may be more competitive with crops (Figures 2.2 and 2.3). Reducing resource availability, increasing management diversity and increasing perennial vegetation in non-cropped areas may be able to mitigate this effect. Management diversity is also likely to reduce selection for ‘crop-mimic’ weeds, and this effect could be enhanced by tailoring management to specifically select against such species.

2.6 Practical opportunities to manipulate ecological processes to increase agroecosystem resilience to weeds

The relationships discussed in the previous two sections indicate that weed quantity and weed quality have opposing responses to management consistency and resource availability (Figure 2.4). Intensive, simplified agroecosystems are characterised by high management consistency and high resource availability, and this tends to promote a high quantity but low diversity of competitive weeds. However, the opposite effect could be achieved by increasing management variability, reducing resource availability and increasing biotic interactions. This suggests that more diverse, complex farming systems that mimic natural ecosystems will be more resilient to weeds over the long term. In this section we explore practical opportunities for achieving such farming systems, and link these practices with ecological processes that maintain weed quantity and weed quality discussed in the previous two sections (Table 2.1). These practical opportunities include some well-known and tried and tested practices, and also newer techniques that may further increase our ability to create agroecosystems that are resilient to weeds.

	Diverse selection pressure	Directional selection pressure	Alternate selection pressure	Appropriate disturbance	Resource availability	Resource diversity	Exploit weed benefits
Crop rotation	✓			✓		✓	
Intercropping/mixed crop stands	✓				✓		
Landscape-scale crop diversity	✓						
Integrated crop-livestock systems	✓		✓			✓	
Competitive and/or cooperative crops		✓	✓		✓		
Perennial crops				✓	✓		
Crop sowing density			✓		✓		
Crop sowing time			✓		✓		
Specific management tools for specific traits		✓					
Precision agriculture techniques					✓		
Encourage natural enemies			✓				
Landscape composition		✓					
Integrate weeds into farming systems							✓

Table 2.1: A summary of practices that increase resilience to weeds outlined in Section 5, and the ecological processes by which they function. To clarify, ‘diverse selection pressure’ indicates techniques that inherently impose a diverse selection pressure and ‘directional selection pressure’ refers to techniques that can be used to deliberately select for specific weed traits or functional types, and ‘alternate selection pressure’ indicates a technique that imposes different selection pressure from conventional weed management practices that can be added to farming systems to further diversify selection pressure.

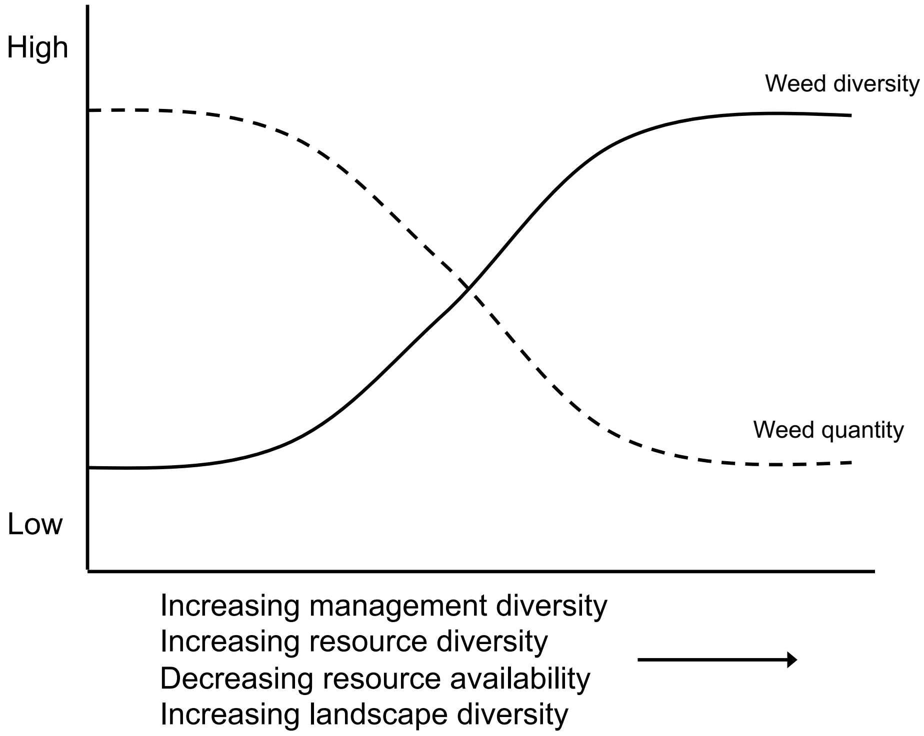

Figure 2.4: Expected relationships between weed quantity, weed diversity, and agroecosystem characteristics, based on the evidence reviewed in the previous two sections. The exact nature of these relationships is not known, but sigmoidal rather than linear relationships were selected to represent the expected relationships because it is unlikely weeds will ever reach zero quantity or diversity and impossible they would reach infinity.

Crop and management diversity in time

There is extensive evidence that crop rotation is a highly effective tool for reducing weed quantity and increasing weed quality (Liebmann and Dyck 1993, Anderson 2005, Davis et al 2012). Different crops require different management practices in terms of the timing and types of seedbed preparation, fertilisation and pest control actions, and thus rotating crops alters the disturbance and resource conditions experienced by weeds each year (Nichols et al 2015, Anderson 2015). This reduces the chance that any species will encounter favourable conditions every year and increases the chance that all species will encounter limits to population growth, and may also sustain diversity through reducing the likelihood that any species will be driven to extinction if it is unable to survive alongside a certain crop or under specific management practices. This can lead to reduced competition between weeds and crops, by reducing selection for crop-mimicking weeds that are adapted to the specific conditions associated with particular crops. Management variation is typically considered to be the most important element of crop rotation for weed management (Smith and Gross 2007), but differences between the crops themselves may also impose further differences in selection pressure on weeds (Smith et al 2015). Crop rotation also creates opportunities to increase resource pool diversity. For example, rotations that incorporate legumes and livestock add different forms of nitrogen to the soil, and diverse plants may release nutrients in other forms through decomposition of biomass or root exudates (Smith et al 2010). This also creates opportunities for weeds to adapt to diverge from crops in resource use patterns, potentially reducing weed-crop competition (Ryan et al 2009).

Crop diversity in space

At a field scale, spatial crop diversity can be increased using mixed crop stands or intercropping practices (Malézièux et al 2015, Isbell et al 2017). Mixed crop stands consist of different varieties of species of crops planted together that can be harvested or utilisedsimultaneously, such as multi-species cover crop mixes, forage crop mixes, or mixed-variety grains. Intercropping consists of different crops planted in the same field but in a spatial arrangement that allows them be harvested at different times or utilised for different purposes. This can involve combinations of field crops, or more complex arrangements such as agroforestry (Malézièux et al 2015). Intercropping as well as mixed crop stands can increase overall resource capture by crops, by incorporating different crop species with complementary patterns of resource use in space and time. Such combinations minimise crop-crop competition and reduce resource availability to weeds (Finn et al 2013, Lowry and Smith 2018).

At a farm or landscape scale, spatial crop diversity can be increased by increasing the number of crops grown simultaneously in different fields. There is evidence that this reduces the area available for weeds to adapt to specific conditions and thus slows the evolution of herbicide resistance (Neve et al 2009), and presumably may also slow the adaptation of weeds to the conditions associated with specific crops. Such effects may also be linked to higher crop spatial diversity being associated with higher crop temporal diversity.

Cultural control: competitive crops, and sowing patterns in time and space

Using crops to suppress weeds presents a distinct selection pressure from those imposed from disturbance-based weed control actions, may select for weeds that diverge from crops in resource use patterns, and is not necessarily associated with additional economic or environmental costs (Andrew et al 2015, Lowry and Smith 2018). The types of crop, as well as their timing, density and arrangement can affect their capacity to compete through reducing resource availability to weeds. Some crop cultivars are inherently capable of greater and more rapid resource capture and thus have a greater suppressive effect on weeds. In annual crops, these tend to be taller cultivars with extensive root systems and high early vigour (Andrew et al 2015). These traits suggest that crops with a ‘faster’ life history strategy are more able to outcompete weeds in annual systems, supporting the idea that a fast life history strategy is the most advantageous in agroecosystem conditions. Competitive crops are thus those that ‘beat weeds at their own game’.

Suppression of weeds by crops can also be increased by increasing sowing density and by sowing arrangements that maximise crop resource capture in space, such as reduced inter-row spacing and intercropping (Weiner et al 2010, Colbach et al 2014b). Such effects may be enhanced by breeding crops for traits that improve their cooperativeness, i.e. total crop resource capture and total yield rather than individual plant fitness (Weiner et al 2010, Weiner 2017). Another innovative breeding avenue for crops to reduce weed pressure is the development perennial field crops. Even if such crops only persist for three or four years, they substantially reduce disturbance and subsequent resource flushes associated with the seedbed preparation, fertilisation and harvest of annual crops. This would limit opportunities for weed establishment compared to annual re-planting (Smith 2015). Breeding for economically viable perennial field crops for temperate regions continues and they may soon be commercially available (Cattani et al 2018, Schlautman et al 2018). Use of the few existing tropical perennial field crop species such as pigeonpea and sorghum could also be upscaled (Peter et al 2017). In annual systems, delayed sowing times or stale seedbeds can be used to ‘trick’ weeds into germinating in the resource flush following a first seedbed preparation, then the seedlings removed in a second disturbance event when the crop is planted. This technique can be effective to limit some weed populations but may result in lower crop yields (Rasmussen 2004), and it is possible the double seedbed preparation and period of bare soil may increase erosion.

Integrated crop-livestock systems

Various economic pressures have driven farms to specialise in either crops or livestock, as agricultural systems have intensified (Sanderson et al 2013). However, specialisation appears to reduce farm sustainability through reducing diversity and thus reducing the ecosystem functions provided by different elements of the agroecosystem (Ewel 1999, Titonell 2014, Isbell et al 2017). Re-integrating livestock and cropping systems may offer a variety of benefits related to energy conservation, nutrient cycling and pest management in both crop and livestock production, as well as diversifying farm products and thus increasing resilience to market fluctuations (Sanderson et al 2013, St-Martin et al 2017).

In terms of weeds, integrating livestock introduces grazing as a direct control method for palatable weed species, which may impose a distinct selection pressure on those weeds through continuous removal of biomass, rather than a single and more often lethal disturbance event imposed by tillage or herbicides. Integrating livestock also increases the incentive for more diverse crop rotations by requiring annual forage crops or multi-year leys to be incorporated into rotations. Both of these could also consist of a diverse mix of crop/forage species to increase spatial crop diversity (Finn et al 2013). Legumes are popular forage crops, and incorporating these could further reduce resource availability to weeds through increasing nitrogen supply from organic sources rather than synthetic fertiliser (Poudel et al 2002), whilst the combination of legumes and livestock manure would increase nitrogen resource diversity (Smith et al 2010).

Specific management tools to select for desired weed traits

In some farming systems, it may be possible to use management actions to directly select for weeds that are less competitive with the specific types of crop grown. In general, the evidence discussed so far suggests that strategies that involve increased management variability and reduced resource availability would select for weeds with a ‘slower’ life history which are expected to be generally less competitive with crops, whilst increased disturbance frequency would select for weeds with a ‘faster’ life history (Figure 2.3). As a more specific example, tall weeds might be expected to be more competitive in systems such as orchards with tall woody perennial crops, due to higher root zone and canopy overlap. Mowing is a management technique that selects for short weeds by removing a disproportionate amount of biomass from taller weeds (Völler et al 2017), and thus including mowing in a management strategy may reduce the competitiveness of weeds with tree or vine crops.

Managing resource availability and diversity

Whilst crop diversity in time and space, crop competitiveness and livestock integration all contribute to reducing resource availability to weeds and increasing diversity, resources can also be managed directly through ‘precision agriculture’ (Pierce and Nowak 1999, Gebbers and Adamchuk 2010). Such an approach requires resources such as fertiliser and irrigation to be applied in locations and at times when they are more likely to be available to crops than weeds, and the resource supplied does not exceed crop requirements. A traditional example is the use of drip irrigation rather than spray irrigation, and technological advances now permit high resolution monitoring of crop condition and resource levels in space and time, so that fertilisers are only applied where and when needed (Diacono et al 2013).

Managing landscape composition and diversity

As discussed with regard to determinants of weed quality, it may be possible to reduce the seed rain of competitive, ‘fast’ *r*-selected species by altering management of non-cropped areas to avoid selecting for these species across so much of the landscape. This could involve planting fencelines and hedgerows with permanent woody cover or with perennial grass and wildflower mixes; the choice of species would depend on the local ecosystem and local biodiversity conservation goals. Increasing landscape complexity and habitat diversity through such measures may have the additional benefit for weed management of increasing the abundance of weed seed predators (see below).

Enhancing weed suppression by natural enemies

Encouraging weed control by natural enemies reduces the effort farmers have to invest in weed control and thus can reduce both economic and environmental costs. Seeds may be an ideal stage of the weed life cycle to target through natural enemies, given that crop seeds do not need to persist in the agroecosystem between seasons, and therefore strategies that increase seed predation would have a low risk of crop damage. Increasing landscape complexity and habitat diversity and implementing no-till practices, retaining crop residues and increasing vegetation cover may further encourage the abundance, diversity and activity of weed seed predators (Menalled et al 2007, Meiss et al 2010, Trichard et al 2013). An advantage of encouraging natural enemies for weed suppression is their capacity to respond in a density-dependent fashion. As weed populations increase, more natural enemies are drawn to the greater food resource, and thus the pressure they apply to reduce that population is increased (Baraibar et al 2012).

Integrating weeds into farming systems

All previous practical techniques discussed have revolved around reducing the negative impacts of weeds on farming through reducing weed quantity and competitiveness, and on increasing positive effects for biodiversity. However, weeds may also have direct positive effects on crop production. For example, Gibson et al (2017) show that weeds can be managed within a corn crop to promote grain quality, which suggests that weeds could be used to raise farm profitability and the nutritional value of food products. In this context, weeds could be considered a spontaneous companion intercrop that improves the quality of the cash crop. Weeds can also be utilised as cover crops, given that the capacity of weeds to cover a field with no effort invested from the farmer may mean they could be a cost-effective way to protect the soil during crop-free periods. They may also contribute to improving soil fertility and breaking pathogen and insect pest cycles (a process exploited by the practice of leaving fallow periods in crop rotations). As we come to understand more about the biology and ecology of weeds, the more we may be able to identify opportunities to use weeds to improve agroecosystem sustainability and to promote crop growth.

2.7 Implications for weed management and weed research

This review has synthesised recent advances in weed ecology to identify practical strategies that increase agroecosystem resilience to weeds through introducing or encouraging processes that naturally limit weed quantity and promote weed quality. Possibilities to integrate these practical strategies into an agroecosystem are illustrated in Figure 2.5. It is evident that diversity in management, resources, biota and landscape composition is essential for resilience to weeds, and would thus form the basis of ecological intensification strategies in weed management. Diversity generates the ecological processes that confer an agroecosystem's ability to self-regulate weed quantity and weed quality. Examples of such processes are diverse crop rotations imposing diverse selection pressures that limit the population increase of different weeds in different years, and natural enemies with density-dependent responses to weeds. In addition to diversity, agroecosystems can also be designed to contain appropriate levels of disturbance and resource availability, as these conditions have potential to maintain weed communities composed of less competitive species with a 'slow' stress-tolerant life strategy (Figure 2.3).

Several of the practical strategies for increasing agroecosystem resilience to weeds described in this review are already successfully implemented in many farming systems across the world, such as crop rotation (e.g. Anderson 2005). This review has provided explanations for their effectiveness in sustainable weed management and confirms the importance of increasing and expanding such practices. Several other tactics that are less widely used are easy to implement at a field or farm scale using existing technologies and available crops, such as increasing rotation diversity, intercropping, mixed crop stands, and targeting management actions to select for specific weeds. Some strategies, such as the re-integration of livestock into cropping systems and the revegetation of non-cropped areas with perennial species, may require larger financial investments by farmers for example to upgrade farm facilities or will require new socioeconomic structures to emerge (Sanderson et al 2013). In order to incentivise such changes, weed researchers have a critical role to play in identifying which strategies are most effective in which systems, using which tools,

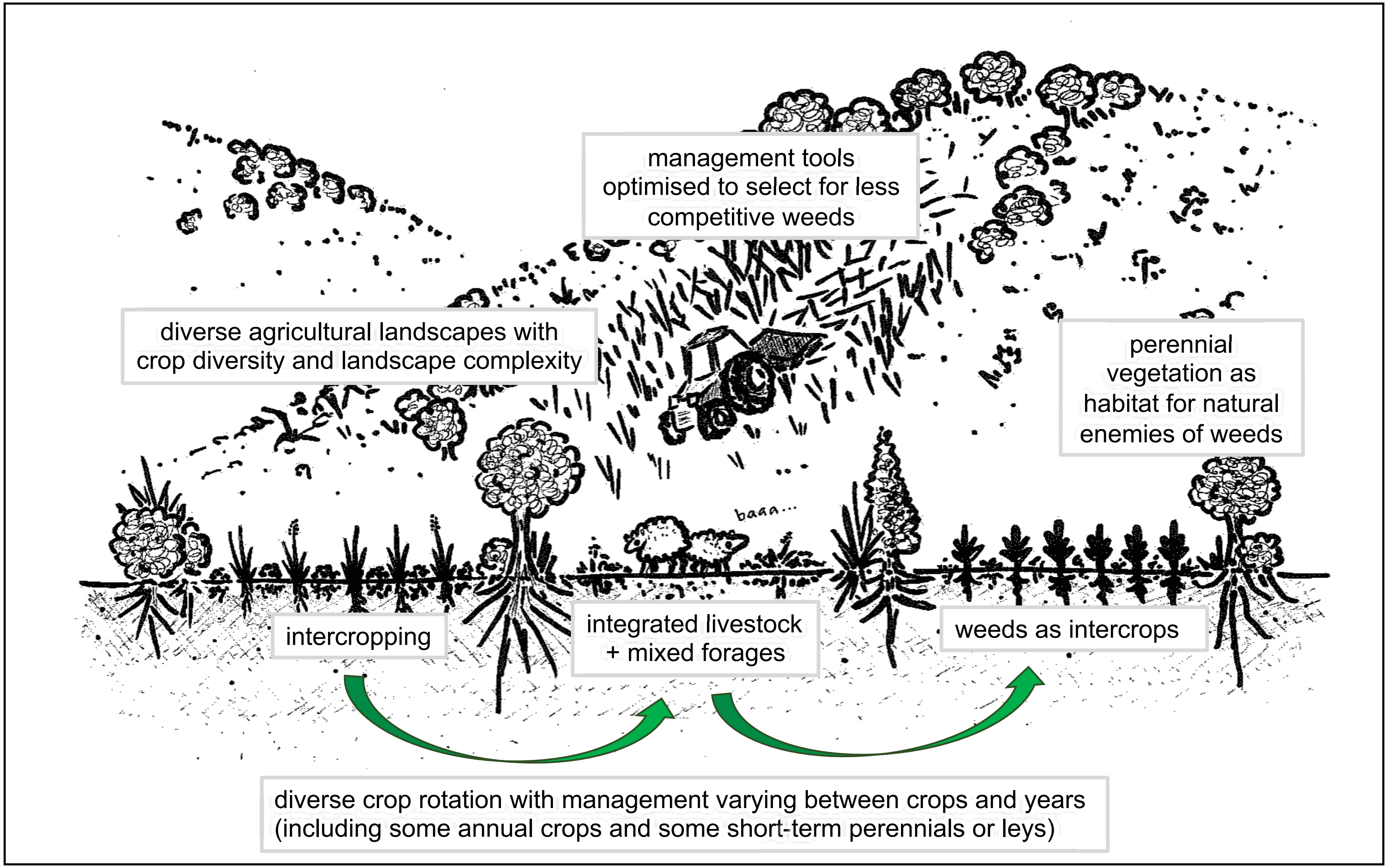

Figure 2.5: A illustration of how agroecosystem resilience to weeds might look in practice.

and in which environments (Kremen and Miles 2012), andcommunicating their findings effectively to farmers (Liebmann et al 2016). It is also important that research, development and extension continues in new techniques that can facilitate the design of resilient agroecosystems, including the breeding of cooperative and/or perennial crops.

To foster the uptake of strategies that increase agroecosystem resilience to weeds whilst reducing environmental impacts, weed research must move away from its fixation on weed control actions such as the use of herbicides (Harker and O'Donovan 2013, Ward et al 2014). Instead the focus needs to be on understanding the interactions between weeds, the agroecosystem and the wider environment. This would allow weed researchers to play a more positive role in increasing the capacity of agroecosystems to conserve biodiversity and ecosystem functioning, and to serve farmers and society by contributing to sustaining both food production and the wider range of life-supporting ecosystem services that we rely on.

2.8 What next for this thesis?

As described in Chapter 1, this thesis explores possibilities for the ecological intensification of weed management to improve agricultural sustainability in South Africa's winter rainfall region. This review chapter has identified a range of ecological processes that can confer agroecosystem resilience to weeds through regulating weed abundance and promoting weed quality, and a range of methods by which these processes can be implemented or harnessed on farms (Table 2.1). The subsequent three chapters explore several of these:

> ***Chapter 3*** explores whether the directional selection imposed by different management practices can promote weed communities of a higher 'quality' in vineyards, in terms of reducing their negative impacts on vines through competition and increasing their potential to support farmland biodiversity;

Chapter 4 investigates the extent to which different crop rotations (with and without integrated livestock) that differ in management diversity and intensity, and in resource availability and diversity, can suppress weed abundance and promote weed diversity;

Chapter 5 investigates whether mixing diverse cover crop species results in increased resource capture by the crop mix (through spatial resource use complementarity), and whether this contributes to suppressing weed abundance and promoting diversity.

These specific practices were chosen out of the list in Table 2.1 for several reasons. Firstly, each has sufficient ecological theory behind it to expect a reasonable degree of success, but none has previously been tested in the context of the ecological processes limiting weed abundance and promoting diversity. Secondly, each practice meets the needs and constraints of farming systems in South Africa's winter rainfall region, and addresses or complements current regional research priorities (Swanepoel, P. and Strauss, J. pers. comm.). Finally, these three practices span a wide range of the ecological theories explored in this review chapter whilst fitting within the logistical and budget constraints of a PhD. The discussion chapter of this thesis will assess how each of the practical chapters contributes to the ecological theory explored in this chapter. It will also evaluate their contributions to practical weed management and agricultural sustainability in South Africa's winter rainfall region, and their implications for taking an ecological approach to weed research and management in general.

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CHAPTER 3: MANAGEMENT PRACTICES INFLUENCE THE COMPETITIVE POTENTIAL OF WEED COMMUNITIES AND THEIR VALUE TO BIODIVERSITY IN SOUTH AFRICAN VINEYARDS

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3.1 Abstract

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 explore how weed communities respond to different management strategies and practices in vineyards of South Africa’s Western Cape. We aim to identify whether any specific practices are associated with weed communities that are less competitive and/or that present a higher value to biodiversity. 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 or mowing, or a combination of these), using ordination and mixed models. Results indicate that management strategies and practices do influence weed community characteristics, acting as filters on both the life history strategies and on specific functional traits of weeds. Compared with herbicides and tillage under conventional management strategies, mown sites on organic vineyards tended to support a higher winter cover of weeds that were shorter, more likely to be native, and more diverse, suggesting that this management approach was most able to minimise weed competitive potential whilst maximising biodiversity value.

3.2 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 environmental risks associated with intensive tillage and herbicide use (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 abundance of weeds is limited by crop production requirements, then for environmental purposes it would be preferable if the weeds that can be retained were of higher value to biodiversity.

Plant ‘response-effect’ functional traits provides 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 in return (Lavorel & Garnier 2002). Farm management actions, as well as local edaphic and climatic 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, weed species possessing these traits may be particularly competitive with crops, given that rapid growth is associated with rapid resource acquisition (Reich 2014), and this would lead to rapid sequestering of resources by weeds away from crops.

The diversity of a weed community can also influence its effect on the surrounding agroecosystem. Species diversity can enhance the diversity, magnitude and resilience of ecosystem functions provided by a community (Díaz & Cabido 2001), and in particular, increased weed community diversity is known to increase support for biodiversity at other trophic levels (Bárberi et al 2010). Farm management actions that select against or promote specific weed traits influence the diversity of the weed community, by filtering out species that do not have the requisite traits for survival. Management actions such as herbicides and tillage that impose high selection pressure for specific traits have a stronger filtering effect, and 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 explore how these characteristics of weed communities are 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), and for local wine farmers improving the conservation value of their vineyards may bring both personal satisfaction and economic benefits (Hamann et al 2015). However, in semi-arid regions such as the Western Cape, water availability in the dry summer is critical for grape production, and thus it is 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 community composition and diversity (e.g. Lososova et al 2002, Baumgartner et al 2007). Weed diversity typically decreases as either soil disturbance or herbicide use increase, indicating a stronger filtering effect on weeds than alternative practices such as mowing (Bruggisser et al 2010, Sanguankeo & León 2011, Kazakou et al 2016). Kazakou et al (2016) demonstrated that the response-effect trait framework can be used to explore how the response traits selected for by management practices link to weed effects on grape production. Their study identified that tillage compared with mowing reduced both weed diversity and weed biomass, and promoted weed species with traits associated with faster growth, although they observed no significant difference in vine water stress or grape yield between treatments.

To assess the potential in Western Cape vineyards to use farm management to select for less competitive weed communities that offered higher biodiversity value, we first explored relationships between weed community composition, farm management, and environmental conditions, to identify the extent to which management could influence the weed community. Secondly, we investigated the links between different management practices and eight weed community characteristics that indicate biodiversity value or competitive potential, aiming to identify whether any specific management practices were associated with a weed community that minimised competitive potential whilst maximising biodiversity value.

3.3 Methods

Study location and layout

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 and 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).

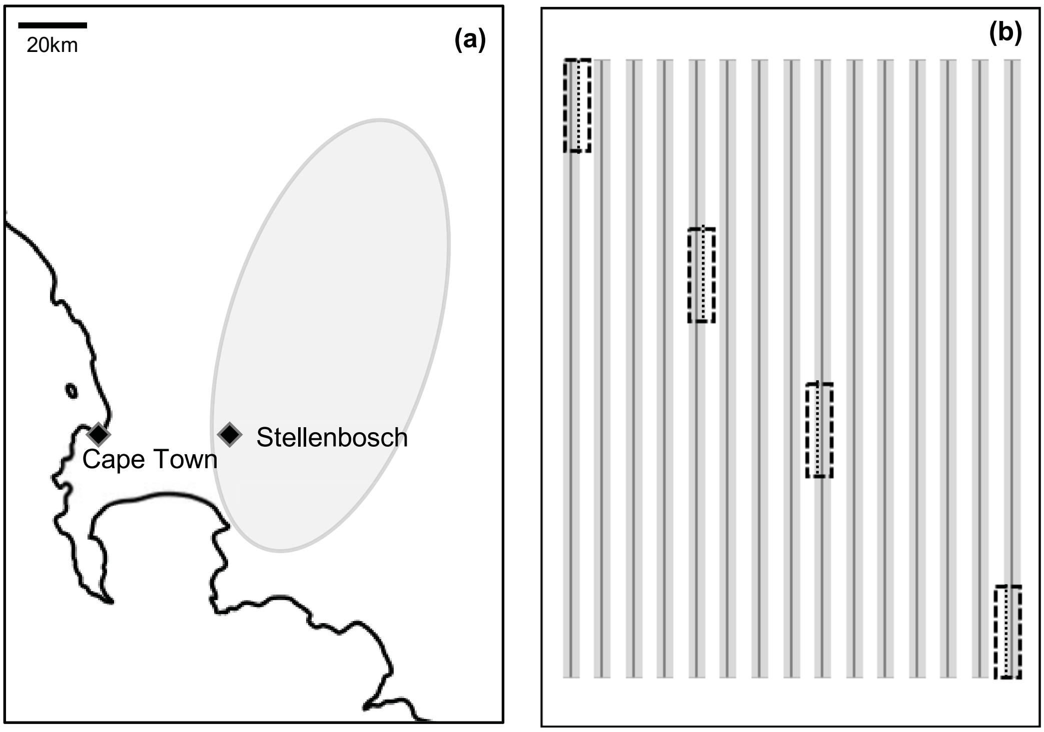

Figure 2.1: (a) Area of the Western Cape in which vineyards included in this study were located. (b) Example layout of survey split-quadrats (dashed black) in each vineyard block, with vine rows shown as dark lines and the vine-row area shaded in grey. The inter-row space is white.

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. At the time of the study, three of the organic vineyards were certified to European Union organic standards while one was undergoing conversion to these standards, although it had been mostly chemical-free for the last six years. On each vineyard, two ‘blocks’ of vines were surveyed: a block is stand of vines of the same cultivar within which management is consistent. Blocks varied in size between vineyards, with smaller blocks approximately 100m long x 50m wide, and larger blocks around 250m x 250m. 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.

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 (Figure 3.1b). Management often differs between the row and inter-row as most farmers prioritise weed control on the rows. This design meant that soil samples (see Section 2.3) 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. Each half of the split quadrat was 1m x 6m (the whole was 2m x 6m). To account for possible variation in the weed community between the edges and centres of blocks (José-María et al 2010), two quadrats were places 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.

Weed surveys took place within a seven-week window between 18/07/2016 and 31/08/2016 to avoid significant changes in composition from early-season to late-season weed species (Hanzlik & Gerowitt, 2016). 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. All variables were collected during this survey period, except for summer weed cover, which was assessed during a follow up survey between 01/12/2016 and 15/12/2016.

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 3.1). 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 classes were converted to numerical scores by taking the mid-point of each cover class (Table 3.1; Lepš & Hadincová 1992).

Table 3.1: 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 and Hadincová 1992).

Eight community characteristics representing the potential competitiveness or potential biodiversity benefits of weeds were selected (Table 3.2). The first four were 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 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.

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) 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. Of these three traits, 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.

Table 3.2: 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).

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

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 3.2). Winter weed cover, native weed cover, and summer weed cover were assessed for each quadrat using visual estimates following the Domin scale. For species diversity, the Shannon diversity index for each quadrat was calculated based on the Domin cover midpoints of each species observed. 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), with 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 was 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%).

Management categories and environmental variables

Measures of environmental variables known to be important to weed community composition (Hanzlik & Gerowitt 2016) were collected from each quadrat according to the methods in Table 3.3. 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 (results summarised in Appendix 1). 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. 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. Tillage is here defined as any disturbance or overturning of at least the top 2cm of soil, and 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 vineyard in which they were located: either organic, low input (maximum one application of glyphosate per year, no other herbicide groups, maximum of one tillage action per year, and manure or compost-based fertilisers only), or conventional (multiple applications and/or multiple herbicide mode-of-action groups, various fertilisation techniques). 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 was thus 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.

Differences in the application of management techniques between vineyards, as well as the use of other weed management practices including cover cropping (inter-rows in five vineyards) and grazing (two vineyards), may have had additional effects on weed composition and community characteristics. However, not every aspect of weed management variation encountered could be accounted for, and so management categories based on the most common practices were selected as the most robust approach to explore whether broad differences in management practices were associated with weed community characteristics.

Table 3.3: 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 and 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.

Data analysis

To assess variation in weed species composition, 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 and assessing the strength of the correlation between the vector and the ordination. Where explanatory variables are categorical factors, group centroids were placed at the average score of each axis for each category. For both continuous variables and factors, the squared correlation coefficient (R^2) was calculated to indicate the goodness of fit between the explanatory variable and ordination space, and the significance of the correlation coefficient was tested using random permutations of the data. The approach of using an NMDS with fitted vectors and centroids 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).

Generalised linear mixed models were used to identify any direct relationships between management type and community characteristics, and between environmental variables and community characteristics. 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. In the management type models, whether or not each site was mown, tilled, or treated with herbicides were included as fixed effects, nested in the overall management strategy of either organic, low input or conventional. Whether or not the sample was located at the edge or centre of the block was also included as a fixed factor. For the models of environmental variables, several of the variables were multicollinear, so the results of fitting environmental vectors to the ordination were used to select variables representative of the main environmental gradients associated with variation in species composition. These were included in the environmental models as fixed effects, using the same quadrat-block-vineyard random effect structure as the management variables.

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). Given the high level of nestedness in the models, sample sizes were too small to conduct post-hoc pairwise comparisons, thus only general trends are discussed in the results. All analyses were undertaken in R, with the ordination implemented in the package *vegan,* and the mixed models using a combination of *lme4, lmerTest* and *afex* (R Core Team 2017).

3.4 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 (Appendix 2). The most widespread and abundant weed was *Lolium* spp., considered by local researchers to be a hybrid complex consisting primarily of *Lolium rigidum,* with contributions from *L. multiflorum* and *L. perenne.* A three-dimensional NMDS ordination was selected to represent the variation in species composition, to reduce stress to below the accepted limit of 0.2 whilst maximising interpretability (Figure 3.2, stress = 0.19). The ordination indicates that management differences are associated with differences in community composition, with sites treated with herbicides associated with a higher abundance of *Lolium* spp. and *Helminthotheca echioides,* mown sites with the native *Melinis repens* and native *Oxalis pes-caprae,* and tilled sites with *Erodium moschatum* and *Raphanus raphanistrum* (Figure 3.2). There is some overlap in composition between sites under different management, and variation within sites with the same management, some of which may be driven by environmental conditions. All environmental fitted vectors were significantly associated with the ordination ($P<0.05$), with the strongest associations between soil texture and rainfall and the second axis (Figure 3.2).

Correlating the community characteristics to the ordination indicated significant relationships between community composition and all community characteristics (Figure 3.2). The results of the mixed models confirm that management strategy and management practices influence community characteristics, notably that mown sites on organic farms tended to

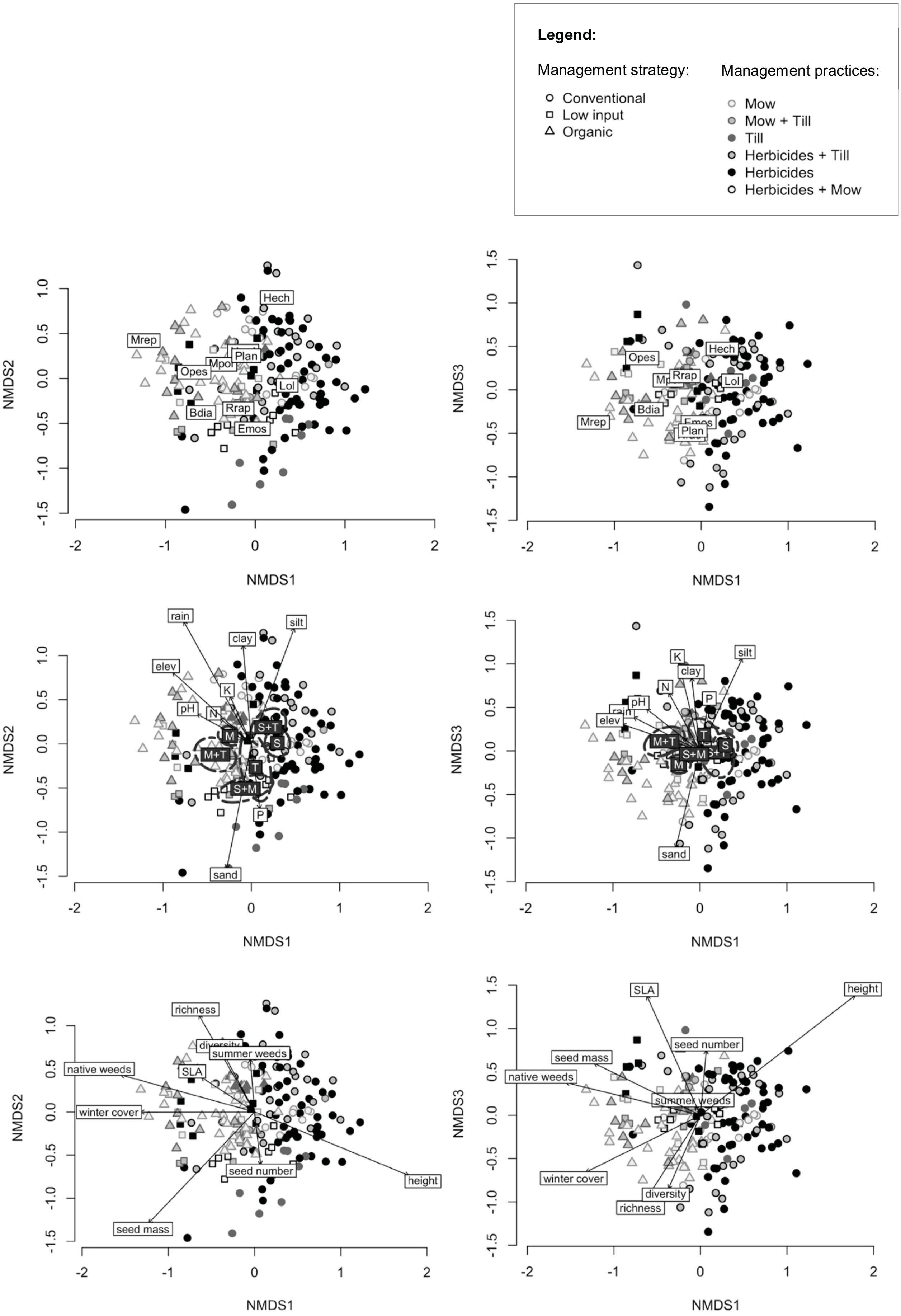
Legend:
Management strategy:
○ Conventional
□ Low input
△ Organic
Management practices:
● Mow
● Mow + Till
● Till
● Herbicides + Till
● Herbicides
○ Herbicides + Mow
NMDS1
NMDS2
NMDS3
Hech
Mrep
Mpor
Plan
Opes
Lol
Bdia
Rrap
Emos
rain
silt
clay
elev
K
pH
N
M
M+T
S+T
S
T
S+M
P
sand
richness
diversity
summer weeds
native weeds
SLA
winter cover
seed number
seed mass
height

Figure 3.2: 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. Sites are colour-coded by the management practices used, and shape-coded by management strategy. The top plots indicate the location of common species based on weighted averages in ordination space (for species name abbreviations see Appendix 2). The centre plots illustrate the fitted vectors for environmental variables and the centroids of different groups of management practices, and the bottom two plots illustrate the fitted vectors of community characteristics. For the centroids, circles indicate the standard error of the mean location of the centroid: where circles do not overlap the locations are significantly different from one another.

have a higher winter and summer weed cover, and organic and low input vineyards had a greater cover by native species (Figure 3.3, Table 3.4). Mown and tilled sites were associated with a higher seed mass, mown sites with shorter weeds, and tilled sites with a higher SLA (Figure 3.3, Table 3.4). No differences were observed between plots located at the edges and centres of blocks (Table 3.4). Environmental variation, represented by rainfall and % sand content, were associated with species richness and winter weed cover, and there is some evidence to suggest that weed height and native weed cover were also influenced by rainfall (Table 3.5).

3.5 Discussion

This study indicates potential for Western Cape vineyard farmers to select for weed communities with certain characteristics through altering management practices. Furthermore, it appears possible to select for a weed community that has both a relatively low competitive potential and a high biodiversity value, supporting previous research that has identified similar optimal possibilities in other farming systems (Storkey 2006, Storkey & Westbury 2007, Mézière et al 2015). A weed community is expected to have higher biodiversity value but lower competitive potential with grapevines if it is more diverse, contains more native species, covers more ground in winter but less in summer, and is composed of shorter species with fewer larger seeds, and a lower SLA. Overall, an organic management strategy appears better able to achieve this than a

Table 3.4: ANOVA F statistics and P-values (based on Satterthwaite Type 3 F tests) for the models of each community characteristic against management practices nested in management strategy (the models included with quadrat nested in block nested in vineyard as random effects). The model for native weed % cover was tested using likelihood ratio due to its Poisson distribution and therefore Chi-square statistics are reported instead of ANOVA F statistics. Symbols next to the P-values highlight significance at P<0.05 (*) or P<0.1 (°).

WINTER WEEDS % COVER	*ANOVA F statistic*	*P-value*
Field	1.5513	0.216
Management strategy	1.6744	0.232
X mow	11.6626	<0.001 *
X till	6.0367	0.004 *
X spray	10.0151	0.002 *
SUMMER WEEDS % COVER	*ANOVA F statistic*	*P-value*
Field	0	0.996
Management strategy	0.6996	0.516
X mow	11.4175	<0.001 *
X till	1.4883	0.243
X spray	0.4326	0.656
NATIVE WEEDS % COVER	*Chi-square value**	*P-value*
Field	1.1461	0.284
Management strategy	0.3226	0.570
X mow	92.7852	<0.001 *
X till	105.5769	<0.001 *
X spray	60.8643	<0.001 *
SPECIES RICHNESS	*ANOVA F statistic*	*P-value*
Field	1.8153	0.182
Management strategy	1.9022	0.195
X mow	1.8233	0.171
X till	1.1765	0.341
X spray	0.5214	0.603
SHANNON DIVERSITY	*ANOVA F statistic*	*P-value*
Field	0.99642	0.321
Management strategy	2.31137	0.140
X mow	2.47489	0.085 °
X till	1.47928	0.245
X spray	2.59947	0.101
HEIGHT CWM	*ANOVA F statistic*	*P-value*
Field	0.4488	0.505
Management strategy	0.1329	0.877
X mow	1.1445	0.355
X till	7.0998	0.002 *
X spray	0.2777	0.761
SLA CWM	*ANOVA F statistic*	*P-value*
Field	1.65277	0.205
Management strategy	0.84078	0.461
X mow	0.78488	0.519
X till	2.45779	0.097 °
X spray	2.48555	0.122
SEED MASS CWM	*ANOVA F statistic*	*P-value*
Field	1.9499	0.165
Management strategy	7.0794	0.006 *
X mow	3.807	0.024 *
X till	6.9797	<0.001 *
X spray	8.1026	0.002 *

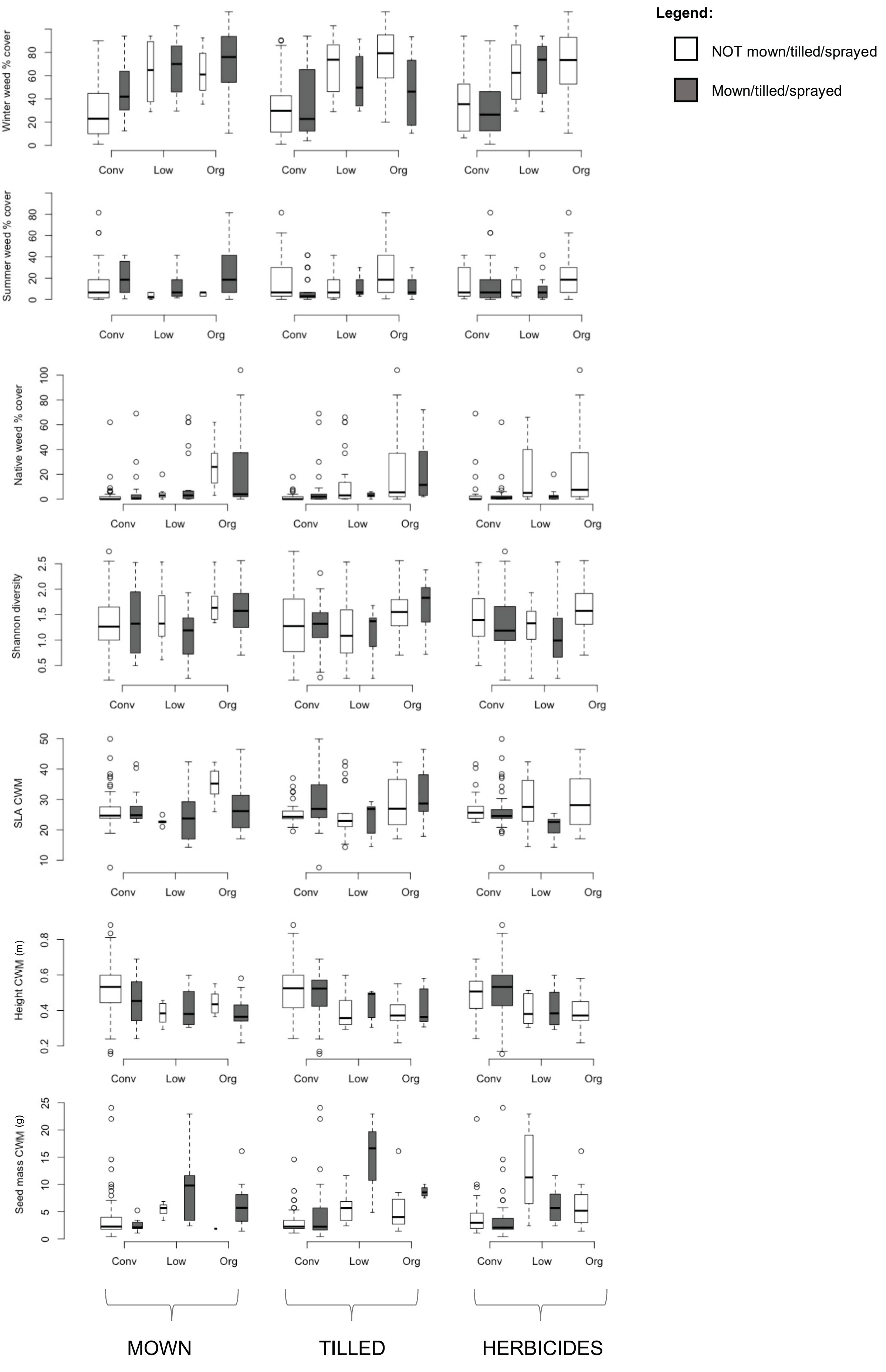
Legend:
NOT mown/tilled/sprayed
Mown/tilled/sprayed
Winter weed % cover
Summer weed % cover
Native weed % cover
Shannon diversity
SLA CWM
Height CWM (m)
Seed mass CWM (g)
Conv
Low
Org
MOWN
TILLED
HERBICIDES

Figure 3.3: Differences between weed community characteristics under different management strategies and practices. Each pair of boxes compares all sites under a specific management strategy (organic/low input/conventional) that were subject to a specific management practice (mowing/tillage/herbicides) against all sites that under the same management strategy not subject to the same practice. Note that there is no herbicide category in the organic management strategy. These plots correspond to the model statistics given in Table 4. Species richness is not illustrated in this figure because no relationships significant to $P<0.1$ were identified.

Table 3.5: Regression coefficients and P-values (based on Satterthwaite Type 3 F tests) for the models of each community characteristic against rainfall and % sand content of soil (the models included with quadrat nested in block nested in vineyard as random effects). The model for native weed % cover was tested using likelihood ratio due to its Poisson distribution and therefore Chi-square statistics are reported instead of ANOVA F statistics. Symbols next to the P-values highlight significance at $P<0.05$ (*) or $P<0.1$ (°).

WINTER WEEDS % COVER	*Regression coefficient*	*P-value*
Sand	6.834	0.034 *
Rainfall	8.749	0.097 °
SUMMER WEEDS % COVER	*Regression coefficient*	*P-value*
Sand	-1.283	0.444
Rainfall	1.961	0.410
NATIVE WEEDS % COVER	*Chi-square value**	*P-value*
Sand	0.786	0.375
Rainfall	2.925	0.087 °
SPECIES RICHNESS	*Regression coefficient*	*P-value*
Sand	-0.031	0.948
Rainfall	1.812	0.048 *
SHANNON DIVERSITY	*Regression coefficient*	*P-value*
Sand	-0.032	0.624
Rainfall	-0.086	0.363
HEIGHT CWM	*Regression coefficient*	*P-value*
Sand	-0.027	0.400
Rainfall	-0.125	0.072 °
SLA CWM	*Regression coefficient*	*P-value*
Sand	-0.011	0.772
Rainfall	0.020	0.696
SEED MASS CWM	*Regression coefficient*	*P-value*
Sand	0.124	0.177
Rainfall	-0.055	0.708

conventional management strategy, and our results suggest that mowing has greater potential to select for such a community than either herbicides or tillage.

Conventional agricultural practices, including the application of synthetic fertilisers and reliance on herbicides and tillage to suppress weeds, are associated with higher resource availability and higher disturbance than organic or low input strategies (José-María et al 2010, Gaba et al 2014). Accordingly, sites in conventional vineyards subject to either herbicides or tillage or both were associated with weed traits indicative of a ‘faster’ life strategy. This response of weed communities to agricultural intensification has been widely observed (Navas 2012, Storkey et al 2012), given that a ‘fast’ life strategy confers an advantage when resources are abundant at germination but become limited by competition as plants mature, and where strong disturbance events select for plants that can grow rapidly to reproduce in windows between disturbance events (Garnier & Navas 2012, Reich 2014).

Specifically, tilled and sites treated with herbicides on conventional vineyards tended to have taller weeds, a trait associated with increased competitive ability for both light and water (Violle at al 2009). Tilled sites also tended to have a higher mean SLA, indicative of faster resource uptake and turnover, while sites treated with herbicides tended to have small seeds, which permit the production of a high number of successful offspring when resources are abundant and competition at the seedling stage is low (Westoby 1998, Garnier & Navas 2012). Such traits are responses to overall resource availability and the disturbance regime; however, the type of disturbance can also select for specific traits. 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 may confer increased survival when subject to harrowing or shallow disc ploughing (the types of tillage typically used by vineyards in this study). In contrast, mown sites on organic vineyards tended to have shorter weeds and intermediate values of SLA and seed mass. Mowing would select directly against tall species by being more likely to remove the growth point and/or a greater quantity of biomass from such species. However, mowing is also a disturbance that does not eliminate all biomass, so seedlings will be subject to some competition from extant weeds, and thus it may be advantageous not to have very small seeds or a very high SLA.

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), and thus 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 high SLA 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 with a low SLA (Storkey et al 2013, Kazakou et al 2016).

Management practices select for traits conferring survival to those practices, and the strength of this selection pressure influences the diversity of a weed community (Gaba et al 2014). Although no conclusive trends were identified in this study, our results suggest that weed diversity tended to be higher on organic farms. This agrees with the findings of previous studies (e.g. José-María et al 2010, Bruggisser et al 2010, Sanguankeo & León 2011), and can be attributed to few weed species possessing the requisite traits to tolerate or resist herbicides. In this study, organic practices were also associated with greater cover by native weed species. Western Cape ecosystems have naturally nutrient poor soils (Coetsee et al 2015), and thus native species may be disadvantaged by the high nutrient availabilities associated with conventional fertilisers. Given that native plants are expected to have stronger relationships with native biodiversity at other trophic levels (McCary et al 2016), shifting vineyard management to more organic practices in the Western Cape could be beneficial to conserve native biodiversity.

This study has 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 such weed communities in vineyards (see also Kazakou et al 2016). We conclude that organic management strategies with mowing as the main weed management tool selects overall for less competitive weeds with higher biodiversity value than either herbicides or tillage: greater diversity, higher winter cover, shorter weeds, and an intermediate SLA. However, a drawback of relying on mowing for weed management in Western Cape vineyards is its limited ability to reduce summer weed cover. If competition for water is of critical concern, this could perhaps be addressed by mowing during the winter, with a single tillage action or herbicide application in late spring. Our results indicate that community composition and characteristics under low input management strategies tended to be similar to those under organic management (Figures 2 and 3), suggesting that limited, judicious use of tillage and herbicides do not counteract the benefits achieved by mowing. Future research on the effects of weeds on grape yields and quality in Western Cape vineyards would be useful to understand the extent to which summer weeds need to be suppressed to sustain profitable grape production.

The composition and characteristics of a weed community can be influenced by environmental conditions as well as by management practices (Hanzlik & Gerowitt 2016). In this study, species composition also varied along a gradient from drier areas with sandier soils low in nutrients to more humid areas with greater soil clay and silt content, and higher nutrient availability. Winter weed cover decreased as soils become 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).

In sum, this study provides a valuable overview of trends in Western Cape vineyard weed communities. We have shown that weed community composition and characteristics do vary in association with management practices, and that potential exists to select for weed communities that have both high value to biodiversity and low competitive potential. To refine how vineyard farmers can maximise biodiversity conservation on their vineyards whilst minimising weed competition, further research would be useful to clarify the effects of weeds and their management on grape yield and quality, and to explore how other trophic levels respond to weed diversity and functional composition. Our findings indicate that organic management practices, and specifically mowing, warrant further investigation as techniques to address the dual goal of minimising both competition and the environmental impacts of weed control.

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3.7 Author contributions

CM designed the study with input from KD and JB. CM undertook the data collection and data analysis and drafted the article, and KD and JB contributed to critically revising the article to produce the final version.

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3.9 Appendix 1: summary of management practices and mean community characteristics

This appendix provides a summary of the management strategies and practices implemented in different vineyards, blocks, rows and inter-rows, and also provides the mean values of each community characteristic for each block (Table 3.6). The second blocks from vineyards 8, 11, and 13 were excluded from the study due to recent substantial changes in management that may have confounded the observed relationship between management and weeds, due to potential persistence in the seedbank of weeds adapted to the previous management practices.

3.10 Appendix 2: checklist of weed species encountered in the surveys.

The list of the 88 identified species from the vineyard surveys (Table 3.7). An additional 26 broadleaved species and one grass species were found that could not be identified. Species listed as "*Genus spp.*" may have included more than one species, where species were difficult to distinguish reliably under field conditions. Species listed as *"Genus sp. A"* or *"Unidentified sp. 1"* are distinct morphotypes that were unable to be identified to species level.

Species occurrence frequency and average cover are provided to indicate which species were most widespread and/or abundant where they occurred, and which were rare. Occurrence is given for both the number of split quadrats, so a species observed on both the row half and interrow half of the same quadrat is counted twice (the total number in the study was 200). Average cover was calculated using the Domin midpoint scores (Table 3.1).

Table 3.6: Summary of the management strategies and practices implemented in different vineyards, blocks, rows and inter-rows, and the mean values of each community characteristic for each block.

MANAGEMENT PRACTICES							MEAN COMMUNITY CHARACTERISTICS FOR EACH BLOCK								
Vineyard	**Block**	**Herbicides**	**Tillage**	**Mowing**	**Other weed management practices**	**Management strategy**	**Winter weeds % cover**	**Summer weeds % cover**	**Native weeds % cover**	**Species richness**	**Shannon diversity**	**Height CWM**	**SLA CWM**	**Seed mass CWM**
1	a	None	None	Rows + interrows	Grazing (cattle)	Organic	95.88	21.94	0.02	12.50	1.62	0.35	19.87	8.27
1	b	None	None	Rows + interrows	Grazing (cattle)	Organic	90.75	18.00	0.04	13.63	1.63	0.37	25.26	4.06
2	a	Rows	None	Interrows		Low input	78.38	2.00	0.43	8.00	1.09	0.35	31.31	5.18
2	b	Rows	None	Interrows		Low input	56.56	11.38	0.13	11.88	1.73	0.40	25.40	5.19
3	a	Rows	None	Interrows		Conventional	17.31	18.31	0.00	4.13	0.81	0.52	23.34	2.07
3	b	Rows	None	Interrows		Conventional	35.19	31.25	0.03	6.75	1.02	0.54	24.64	2.44
4	a	Rows only	None	Interrows		Conventional	43.00	29.19	0.04	17.75	2.10	0.38	27.66	3.27
4	b	Rows only	None	Interrows		Conventional	38.25	27.00	0.05	14.88	1.96	0.36	25.80	1.74
5	a	None	Rows	Interrows	Grazing (cattle)	Organic	58.25	21.44	0.51	16.25	1.73	0.38	37.62	2.76
5	b	None	Rows	Interrows	Grazing (cattle)	Organic	73.94	31.44	0.36	13.75	1.46	0.47	33.13	1.94
6	a	Rows only	Alternate interrows	Rows + interrows	Cover crops (alternate interrows)	Low input	68.56	14.25	0.05	7.63	0.74	0.40	19.22	12.08
6	b	Rows only	Alternate interrows	Rows + interrows	Cover crops (alternate interrows)	Low input	57.19	13.50	0.05	7.25	1.17	0.49	24.04	8.83
7	a	Rows + interrows	Alternate interrows	None	Cover crops (alternate interrows)	Conventional	23.75	1.13	0.04	5.88	1.06	0.50	30.62	7.35
7	b	Rows + interrows	Alternate interrows	None	Cover crops (alternate interrows)	Conventional	32.75	7.81	0.24	6.38	1.06	0.50	31.27	8.31
8	b	None	Interrows	Rows + interrows	Cover crops (interrows)	Organic	33.44	19.50	0.18	9.50	1.84	0.48	27.53	5.12
9	a	None	Interrows	Rows + interrows		Organic	56.69	18.50	0.45	12.38	1.63	0.28	25.11	4.35
9	b	None	Interrows	Rows + interrows		Organic	76.94	16.33	0.67	7.50	1.13	0.35	33.34	10.02
10	a	Rows	Interrows	None	Cover crops (interrows)	Conventional	20.88	4.50	0.01	5.00	1.02	0.62	24.53	4.47
10	b	Rows	Interrows	None	Cover crops (interrows)	Conventional	31.88	7.13	0.06	7.88	1.42	0.54	29.34	6.89
11	b	Rows only	Interrows	Interrows		Conventional	37.88	16.19	0.25	7.38	1.32	0.64	30.95	1.99
12	a	Rows + interrows	Interrows	None	Cover crops (interrows)	Conventional	28.69	15.38	0.12	7.00	1.13	0.59	24.12	2.47
12	b	Rows + interrows	Interrows	None	Cover crops (interrows)	Conventional	35.69	17.00	0.03	6.75	1.07	0.56	15.72	2.11
13	a	Rows + interrows	Interrows	None		Conventional	43.75	5.63	0.06	11.00	1.51	0.26	21.25	1.49
14	a	Rows + interrows	Interrows	None		Conventional	54.50	4.06	0.01	8.63	1.16	0.55	23.85	2.72
14	b	Rows + interrows	Interrows	None		Conventional	27.50	1.81	0.17	9.88	1.69	0.43	21.72	2.08

Table 3.7: Checklist of all weed species encountered in this study.

Species	**Code**	**Family**	**Occurrence: number of quadrats (as % of total quadrats)**	**Average % cover across all quadrats**	**Notes**
Anagallis arvensis	Aarv	Primulaceae	43 (21.5)	0.23	
Arctotheca calendula	Acal	Compositae	33 (16.5)	0.34	
Avena barbata	Abar	Poaceae	12 (6)	0.23	
Avena spp	Aspp	Poaceae	50 (25)	0.56	*A. fatua* and *A. sativa*
Bidens pilosa	Bpil	Compositae	2 (1)	0.01	
Bromus diandrus	Bdia	Poaceae	75 (37.5)	5.31	
Bulbostylis	Bsp	Cyperaceae	15 (7.5)	0.09	
Carduus pycnocephalus	Cpyc	Compositae	5 (2.5)	0.02	
Chenopodium album	Calb	Amaranthaceae	7 (3.5)	0.04	
Cirsium vulgare	Cvul	Compositae	13 (6.5)	0.10	
Convolvulus arvensis	Carv	Convolvulaceae	2 (1)	0.02	
Conyza sumatrensis	Csum	Compositae	33 (16.5)	0.33	
Cotula turbinata	Ctur	Compositae	24 (12)	0.23	
Cynodon dactylon	Cdac	Poaceae	16 (8)	0.58	
Digitaria sanguinalis	Dsan	Poaceae	18 (9)	0.55	
Echium plantagineum	Epla	Boraginaceae	10 (5)	0.38	
Eleusine indica	Eind	Poaceae	3 (1.5)	0.04	
Erharta longiflora	Elon	Poaceae	15 (7.5)	0.38	
Eriocephalus africanus	Eafr	Compositae	2 (1)	0.07	
Erodium moschatum	Emos	Geraniaceae	82 (41)	2.76	
Euphorbia inaequilatera	Eina	Euphorbiaceae	17 (8.5)	0.22	
Euphorbia peplus	Epep	Euphorbiaceae	43 (21.5)	0.34	
Foeniculum vulgare	Fvul	Apiaceae	5 (2.5)	0.01	
Fumaria officinalis	Foff	Papaveraceae	11 (5.5)	0.04	
Galium spurium	Gspu	Rubiaceae	4 (2)	0.02	
Geranium molle	Gmol	Geraniaceae	50 (25)	0.47	
Helminthotheca echioides	Hech	Compositae	61 (30.5)	1.86	
Hordeum vulgare	Hvul	Poaceae	5 (2.5)	0.02	
Hypochaeris glabra	Hgla	Compositae	6 (3)	0.09	
Hypochaeris radicata	Hrad	Compositae	83 (41.5)	1.44	
Kickxia elatine	Kela	Plantaginaceae	7 (3.5)	0.02	
Kickxia spuria	Kspu	Plantaginaceae	2 (1)	0.01	
Lactuca serriola	Lser	Compositae	27 (13.5)	0.15	
Lamium spp.	Lam	Lamiaceae	27 (13.5)	0.24	*L. amplexicaule* and *L. purpureum*
Laphangium luteoalbum	Llut	Compositae	6 (3)	0.03	

Lepidium africanum	Lafr	Brassicaceae	3 (1.5)	0.01	
Lolium spp.	Lol	Poaceae	158 (79)	11.34	Hybrid complex of thought to be primarily *L. rigidum* with contributions from *L. perenne, L. multiflorum* and *L. temulentum*
Lupinus angustifolius	Lup	Fabaceae	6 (3)	0.03	
Malva parviflora	Mpar	Malvaceae	6 (3)	0.34	
Medicago polymorpha	Mpol	Fabaceae	76 (38)	2.17	
Medicago sativa	Msat	Fabaceae	1 (0.5)	<0.01	
Medicago scutellata	Mscu	Fabaceae	10 (5)	0.14	
Medicago truncatula	Mtru	Fabaceae	20 (10)	0.83	
Melinis repens subsp. repens	Mrep	Poaceae	17 (8.5)	1.35	
Moraea ciliata	Mcil	Iridaceae	6 (3)	0.04	
Nerium oleander	Nole	Apocynaceae	1 (0.5)	<0.01	
Oenothera indecora	Oind	Onagraceae	5 (2.5)	0.06	
Oenothera rosea	Oros	Onagraceae	10 (5)	0.08	
Ornithopus sativus	Osat	Fabaceae	2 (1)	0.01	
Oxalis corniculata	Ocor	Oxalidaceae	4 (2)	0.01	
Oxalis pes-caprae	Opes	Oxalidaceae	93 (46.5)	6.80	
Paspalum urvillei	Purv	Poaceae	9 (4.5)	0.15	
Pelargonium sp. A	PspA	Geraniaceae	1 (0.5)	<0.01	
Pelargonium sp. B	PspB	Geraniaceae	2 (1)	0.01	
Pennisetum clandestinum	Pcla	Poaceae	17 (8.5)	0.12	
Plantago lanceolata	Plan	Plantaginaceae	105 (52.5)	2.64	
Poa annua	Pann	Poaceae	3 (1.5)	0.01	
Polycarpon tetraphyllum	Ptet	Caryophyllaceae	10 (5)	0.53	
Polygonum aviculare	Pavi	Polygonaceae	24 (12)	0.25	
Raphanus raphanistrum	Rrap	Brassicaceae	12 (6)	0.07	
Rubus sp. A	RspA	Rosaceae	104 (52)	1.76	
Rumex acetosella	Race	Polygonaceae	4 (2)	0.03	
Rumex crispus	Rcri	Polygonaceae	1 (0.5)	<0.01	
Rumex obtusifolius	Robt	Polygonaceae	4 (2)	0.02	
Senecio arenaria	Sare	Compositae	4 (2)	0.02	
Senecio pterophorus	Spte	Compositae	34 (17)	0.18	
Senecio sp. A	SspA	Compositae	5 (2.5)	0.02	
Senecio sp. B	SspB	Compositae	2 (1)	0.01	
Senecio vulgaris	Svul	Compositae	20 (10)	0.08	
Seriphium plumosum	Splu	Compositae	1 (0.5)	0.01	
Silene gallica	Sgal	Caryophyllaceae	9 (4.5)	0.11	
Sinapis alba	Salb	Brassicaceae	2 (1)	0.02	
Solanum nigrum	Snig	Solanaceae	2 (1)	0.02	

Sonchus oleraceus	Sole	Compositae	77 (38.5)	0.37
Spergula arvensis	Sarv	Caryophyllaceae	1 (0.5)	0.00
Stellaria media	Smed	Caryophyllaceae	10 (5)	0.22
Tagetes minuta	Tmin	Compositae	17 (8.5)	0.20
Torilis nodosa	Tnod	Apiaceae	18 (9)	0.14
Trifolium alexandrinum	Tale	Fabaceae	2 (1)	0.01
Trifolium arvense	Tarv	Fabaceae	5 (2.5)	0.02
Trifolium incarnatum	Tinc	Fabaceae	5 (2.5)	0.02
Trifolium repens	Trep	Fabaceae	9 (4.5)	0.06
Trifolium subterraneum	Tsub	Fabaceae	16 (8)	0.15
Trifolium vesiculosum	Tves	Fabaceae	7 (3.5)	0.03
Veronica persica	Vper	Plantaginaceae	22 (11)	0.14
Vicia faba	Vfab	Fabaceae	1 (0.5)	<0.01
Vicia sativa	Vsat	Fabaceae	24 (12)	0.16
Vicia spp.	Vspp	Fabaceae	37 (18.5)	0.42
x Triticosecale	Trit	Poaceae	5 (2.5)	0.03
Anagallis arvensis	Aarv	Primulaceae	43 (21.5)	0.23
Arctotheca calendula	Acal	Compositae	33 (16.5)	0.34

CHAPTER 4: LIVESTOCK IN DIVERSE CROPPING SYSTEMS IMPROVE WEED MANAGEMENT AND SUSTAIN YIELDS WHILST REDUCING INPUTS

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4.1 Abstract

Intensive cropping systems select for a low diversity of weeds tolerant of chemical control, leading to persistent weed-crop competition and declining biodiversity. Crop rotation can mitigate this by introducing variable filters on the weed community through increasing management diversity. In this study we investigate the effect of integrating livestock into no-till crop rotations to complement chemical weed control. We analysed twelve years of weed seedbank data from a trial of eight rotation systems with different crop sequence diversities, of which four included grazed forage phases. Linear mixed models and ordination were used to assess how weed abundance, diversity and community composition responded to management filters, defined in terms of levels of disturbance strength and diversity (grazing and herbicides), and resource availability and diversity (inorganic fertilisers, legumes and manure). Grazed rotation systems had less herbicide applied than ungrazed rotation systems, and had the lowest weed abundance and highest weed diversity. Herbicides and grazing apply contrasting selection pressures on weeds, and this combination was more effective in reducing weed pressure than increasing herbicide quantity or mode-of-action diversity. Lower resource availability and higher nitrogen source diversity in grazed systems may have further reduced weed abundance and promoted diversity. Crop sequence diversity also reduced weed abundance and promoted weed diversity, indicating that variable crop-weed interactions can enhance weed management. In addition, yields in the main cash crop (wheat) were highest where crop diversity was highest, regardless of whether the system contained grazed phases. Diverse rotation systems produced high yields, and the inclusion of grazed forage phases maintained these yields at lower applications of herbicides and fertilisers: integrated livestock can therefore improve the sustainability of no-till systems. The role of grazing as a filter imposing a contrasting selection pressure to other weed control options could be further explored to improve weed management in different farming systems.

4.2 Introduction

In recent decades, farming systems have become increasingly specialised to produce a small number of crops on large scales in short rotations, and to separate crop production from livestock production. This has been facilitated by the introduction of high yielding cultivars in a few major crops, inorganic fertilisers, pesticides and specialised equipment. However, the long-term prospects of this ‘Green Revolution’ are in doubt: the environmental impacts and the tendency of such systems to select for a small number of highly injurious pests, weeds, and diseases, have led to recent calls for the re-diversification of cropping systems as part of the drive for ‘sustainable intensification’ (Pretty and Barucha 2014). Increasing cropping system diversity can increase both agricultural productivity and sustainability (Isbell et al 2017), and diverse crop rotations in particular have been shown to improve soil fertility, suppress pests and diseases, support beneficial biodiversity, and stabilise incomes (Davis et al 2012, Wezel et al 2014). These benefits may be further enhanced by re-integrating cropping and livestock systems (Sanderson et al 2013, St-Martin et al 2017).

Long-term experiments that investigate the functions of diversity across whole farming systems make an important contribution to re-diversification, by enabling the study of processes that manifest over decadal time scales, such as weed community dynamics (Paul et al 1998, Storkey et al 2016). Previous findings indicate that the multiple benefits of crop rotations can result from the different ecological and economic properties of different crops, but are often also driven by variation in management associated with different crops (Davis et al 2012, Gaba et al 2013, Wezel et al 2014). Intensive cropping systems lacking in management variation tend to have weed communities dominated by only a few species with strongly ruderal traits that confer advantage in resource-rich, frequently disturbed environments (Storkey et al 2010, Storkey et al 2012, Reich 2014), and herbicide resistant species are also common (Neve et al 2009, Mortensen et al 2012). This indicates that consistent management actions reduce weed diversity, but fail to suppress species tolerant to those actions. Weed-crop competition therefore persists, despite substantial investment in weed control, whilst the ecosystem services offered by a diverse weed community are lost (Petit et al 2015, Gaba et al 2016).

Crop management actions can be interpreted as filters on the weed community, allowing species that possess traits conferring tolerance to the disturbances and conditions imposed by management to thrive, and limiting the survival of those that do not. Varying management between years alters the pattern of this selection pressure each year, reducing the chance that any single weed species is driven to extinction, but increasing the chance that all species would encounter limits to their survival and reproduction at some point (Booth and Swanton 2002, Navas 2012). This also limits the opportunities for weeds to adapt to a consistent set of conditions, as has occurred with the evolution of herbicide resistance in response to the frequent cultivation of a limited number of crops reliant on a small range of herbicide active ingredients (Neve et al 2009, Mortensen et al 2012).

Several studies have shown that crop rotations involving differences in the techniques and timings of sowing, harvest, soil preparation and herbicide use are effective for weed management (Anderson 2015, Blackshaw et al 2015, Petit et al 2015). However, it remains unclear whether crop rotation itself is sufficient, if different crops are not associated with different management (Smith and Gross 2007, Mortensen et al 2012). In this context, a major limitation of the recent spread of no-till cropping practices is the loss of tillage as a weed control option, and the reliance of these systems on herbicides. One option to increase the diversity of weed selection pressure in no-till systems is to integrate livestock, by adding grazed forage crop phases to the rotation. This practice is widespread in some regions of the world and appears profitable for farmers, but remains relatively understudied with regard to weed management (Sanderson et al 2013). Grazing would be expected to directly suppress weeds, and in addition, the combination of a forage legume and livestock manure may further enhance weed diversity through increasing nitrogen resource diversity (Smith et al 2010).

In this study, we compared long-term weed seedbank trends between rotation systems with different crop sequence diversities, and between crop-only systems and integrated crop-livestock systems. Ungrazed systems with low crop diversity were subject to agrichemical-intensive management, resulting in a strong consistent disturbance induced by herbicides, and high resource availability from fertilisers. In contrast, diverse systems with livestock incorporated grazing, legumes, herbicides and fertilisers, resulting in more diverse disturbances and nutrient sources. By comparing the different rotation systems, we thus explored the following hypotheses:

(1) The diversity of management filters (disturbance diversity and resource diversity) reduces weed abundance and increases weed diversity.

(2) The strength of management filters (disturbance intensity and resource availability) increases weed abundance and reduces weed diversity.

4.3 Methods

Trial location, layout and timing

This study used weed seedbank data from the Langgewens Long-Term Crop Rotation Trial, which investigates the agronomic performance of eight different crop rotations under conservation agriculture practices. The trial is located in South Africa's Western Cape Province (33°17'0.78"S, 18°42'28.09"E; Figure 4.1). The site receives an average annual rainfall of 376mm, with approximately 80% received during the winter months. This constrains regional production to one crop per year, sown in April and harvested in November, with a fallow period over summer. The trial began in 1996, but weed data was only systematically collected across all systems since 2005, thus the twelve years in this study span 2005 - 2016. The eight systems are each replicated twice in a randomised block design, and within each replication all crop types are planted each year in the order of the specified rotation (Table 4.1). See the appendix (Section 4.9) for a full explanation of the trial design. Plot sizes vary between 0.5 and 2 ha, depending on the system diversity and whether the system is grazed, but the data used here is based on weed seeds collected in the same amount of soil from each plot, so plot size would not affect the sample. The use of seedbank data allowed us to quantify trends without the confounding effect of stochastic processes that can influence the emerged weed flora in any given year.

Crop species included in the trial are wheat *(Triticum aestivum),* canola *(Brassica napus),* lupins *(Lupinus angustifolius),* and annual self-regenerating medic species *(Medicago truncatula and M. polymorpha)* and white clover *(Trifolium repens)* (Table 4.1). Wheat and canola function as cash crops, lupins as ungrazed cover crops (with seeds harvested for income), and annual self-regenerating medics and clovers as forage crops grazed by sheep *(Ovis aries),* at a stocking rate of four sheep ha^{-1} (standard local practice; Basson 2017). Sheep are moved onto the forage crops when the medic and clover pastures begin to establish in April or May (these regenerate each year but are sprayed off in cash crops). In system H, sheep are kept aside in additional pastures to forage on saltbush *(Atriplex nummularia)* for approximately six weeks until the annual medic/clover mix has reached at least 90% groundcover. Sheep also graze winter crop residues over the summers in systems E-H, and are occasionally used for short periods (four to five days) toward the end of the summer fallow period in the ungrazed systems, as their trampling can break up high residue loads to ease planting. This is done before the first rains and prior to planting, and the lack of summer rainfall in the region means that few, if any, weeds are present at this time and thus briefly introducing sheep in this way would have minimal impact on weeds in otherwise ungrazed systems. All rotation systems are managed according to local best practices and industry recommendations, resulting in variation in agrichemical use between rotation systems and over time (Fig.ig. 2). From 1996 to 2001, the trial was under minimum-tillage (a disc harrow was used to prepare the seedbed), and since 2002 the trial has been under no-till practices with a tine planter.

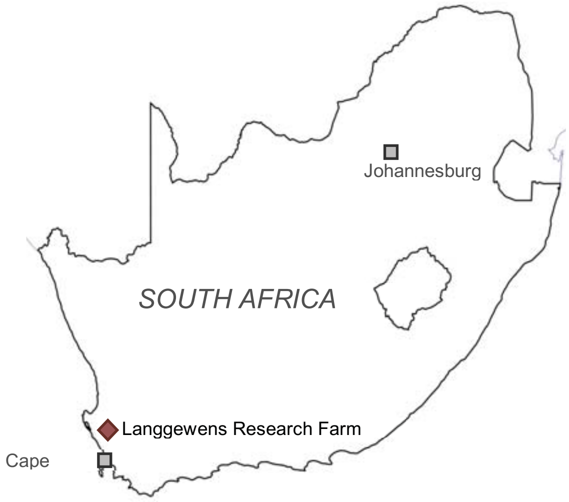


Figure 4.1: The location of Langgewens Research Farm in the Western Cape, South Africa.

Table 4.1: The composition of the crop rotations in the eight different rotation systems included in the Langgewens Long-Term Crop Rotation Trial. Crop phases marked with (G) were grazed by sheep.

Code	Rotation system
A	Wheat – Wheat – Wheat – Wheat
B	Wheat – Wheat – Wheat – Canola
C	Wheat – Canola – Wheat – Lupins
D	Wheat – Wheat – Lupins – Canola
E	Wheat – Medic (G) – Wheat – Medic (G)
F	Wheat – Medic/clover mix (G) – Wheat – Medic/clover mix (G)
G	Medic (G) – Wheat – Medic (G) – Canola
H	Wheat – Medic/clover mix* (G) – Wheat – Medic/clover mix* (G) **with saltbush pastures to rest medic/clover pastures*

Data collection

Weed seedbank samples

Seedbank samples were collected in late March or early April prior to planting each year. From each plot, 80 soil cores of 105 mm diameter and 5 cm depth were combined to form a single sample. The experiment is a no-till system so weed seeds were assumed to be concentrated in this surface layer. Directly following sampling, the soil was placed in 400x250mm trays in a layer approximately 20mm thick over sterilised river sand, under shade-nets with regular irrigation to promote germination. Seedlings that emerged were counted with removal between two and four times until September. Occasionally seedlings could not be identified; these constituted 4.3% of the seedlings observed and were not included in the dataset. ‘Volunteer’ seedlings belonging to the crop species used in the trial were also not included. This direct germination method was used rather than a seed extraction method due to the lower risk of under-representing species with small and light-coloured seeds (Gross 1990). Both methods are suitable for detecting seedbank changes in response to agricultural management (Ball and Miller 1989).

During the twelve-year timeframe each plot completed three full four-year rotations, allowing the seedbank to be assessed at the level of the whole rotation with three time periods. Seedling counts were averaged across each four-year rotation period: 2005 to 2008 = Period 1, 2009 to 2012 = Period 2, and 2013 to 2016 = Period 3. ‘Weed abundance’ subsequently refers to the average number of seedlings per year within each period. ‘Weed diversity’ is the average species diversity of seedlings per year, calculated using Fisher’s log series alpha. This diversity index is insensitive to differences in abundance (Magurran 2003), and was selected due to large differences in weed abundance between treatments.

Agronomic data

The amount of fertilisers and herbicides applied to each plot were aggregated to a total amount per hectare over each four-year period. Herbicide quantities were standardised within each active ingredient (to the proportion of the maximum dose of that ingredient applied in the trial) to take account of differences in potency among different active ingredients. Wheat was harvested each year with a combine harvester, and the yield (wet grain weight standardised to 14% moisture) for each plot was converted to the proportion of the average yield within the trial for that year. This accounted for inter-annual yield variation in response to climate variables such as rainfall, allowing any consistent effect of rotation system on yield to be identified across different years.

Data analyses

All analyses were undertaken in *R* Version 3.4.3 (R Core Team 2017)*,* using the packages *lme4, afex, lsmeans, effects* and *vegan.* Prior to analyses, weed abundance was converted to the natural logarithm of the abundance plus one.

Differences in weed abundance, weed diversity, and wheat yield between systems

Differences in weed abundance, diversity and wheat yield between rotation systems were investigated using linear mixed regression models. As fixed effects, the models for weed abundance and diversity included the main effects and interaction terms for rotation system and period. The wheat yield model included only rotation system, as variation between periods had been accounted for by using yields standardised within each year. Plot was included in all models as a random effect to account for repeated measures in the same plot over time. P-values for the significance of fixed effects were calculated using parametric bootstrapping, one of the most reliable methods for mixed models (Halekoh and Højsgaard 2014). This approach involves comparing differences between the full model and sub-models, and thus does not generate P-values for each level of a factor, only whether the effect of the factor is significant overall. Tukey’s pairwise comparisons were used to assess differences between the different rotations and periods in each model. Differences could thus be assessed between low and high crop diversity within either the ungrazed or grazed systems, or between grazed and ungrazed systems or either lower or higher crop diversities.

Differences in weed abundance and diversity in response to filter strength and filter diversity

The same modelling approach as above was employed to explore how weed abundance and diversity responded to differences in crop sequence diversity, herbicides, fertilisers, and grazing. These variables were used to explore the two hypotheses of this study regarding filter strength and filter diversity. The presence or absence of grazing and the number of herbicide mode-of-action groups used indicated the diversity of disturbances, while the amount of herbicide applied (grams of active ingredient per hectare) represented the strength of the herbicide disturbance. Grazing pressure differed slightly in strength only in system H, where sheep grazed the medic/clover pastures for approximately 20% less duration each season, but otherwise all grazed systems had two forage phases with four sheep ha^{-1}. To minimise the complexity of the analyses, grazing was included as either ‘present’ or ‘absent’, but the reduced duration in system H was noted when interpreting the results.

The number of nitrogen sources available represented resource diversity: these were synthetic nitrogen fertiliser, nitrogen released from legume crops, and nitrogen circulated to soil through sheep manure and urine. The amounts of synthetic nitrogen, phosphorus and potassium fertiliser applied were considered indicators of maximum resource availability. The trial is managed to provide adequate nutrition to each crop through fertilisers, crop residues and/or livestock manure, and thus the overall quantity of nutrients that become available over the season within each system can be assumed to be similar. However, research suggests that nutrients from organic sources such as crop residues and manure are released gradually over the season, whilst synthetic fertilisers provide a flush of nutrients at the time of application, and thus a high peak of nutrient availability (Poudel et al 2002, Crews and Peoples 2005). Furthermore, this peak would occur early in the season when the majority of fertiliser is applied, when crop seedlings are too small to efficiently capture nutrients and competition imposed on weeds would be weak. A higher maximum nutrient availability resulting from higher fertiliser applications is therefore expected to increase weed abundance and reduce weed diversity, whereas the longer duration but lower maximum resource availability resulting from nitrogen resource diversity is expected to be associated with fewer weeds with a greater diversity.

Crop sequence diversity was also included to assess whether it had an independent effect on weeds in addition to the disturbance and resource variables. Within-year diversity (i.e. the medic/clover mix in systems F and H) was not assessed, nor were the saltbush in system H, as these perennial shrubs were located on separate plots outside the rotation.

Indices for each of the above variables were calculated for each plot in each period and scaled to between 0 and 1 (Table 4.2; Figure 4.2) to standardise the different metrics of disturbance. All variables, except for crop sequence diversity, were collinear (detected through high variance inflation factors) and could not be included in the same model. Different models were therefore constructed for each collinear variable, and contained period, crop sequence diversity, the variable of interest, and the interaction between crop diversity and the variable of interest. No interaction with period was included as there was no significant interaction between rotation system and period in the previous set of models, thus it was not logical to expect period to interact with management differences between rotations. Plot was again included as a random effect. The results of these models were interpreted by investigating a) whether each variable was significant using the P-values calculated by parametric bootstrapping, and b) whether any models had a better fit than others, by comparing their Akaike Information Criteria (AIC). All linear mixed models were fitted using maximum likelihood, as opposed to restricted maximum likelihood, to ensure that parametric bootstrapping and AIC comparisons were valid.

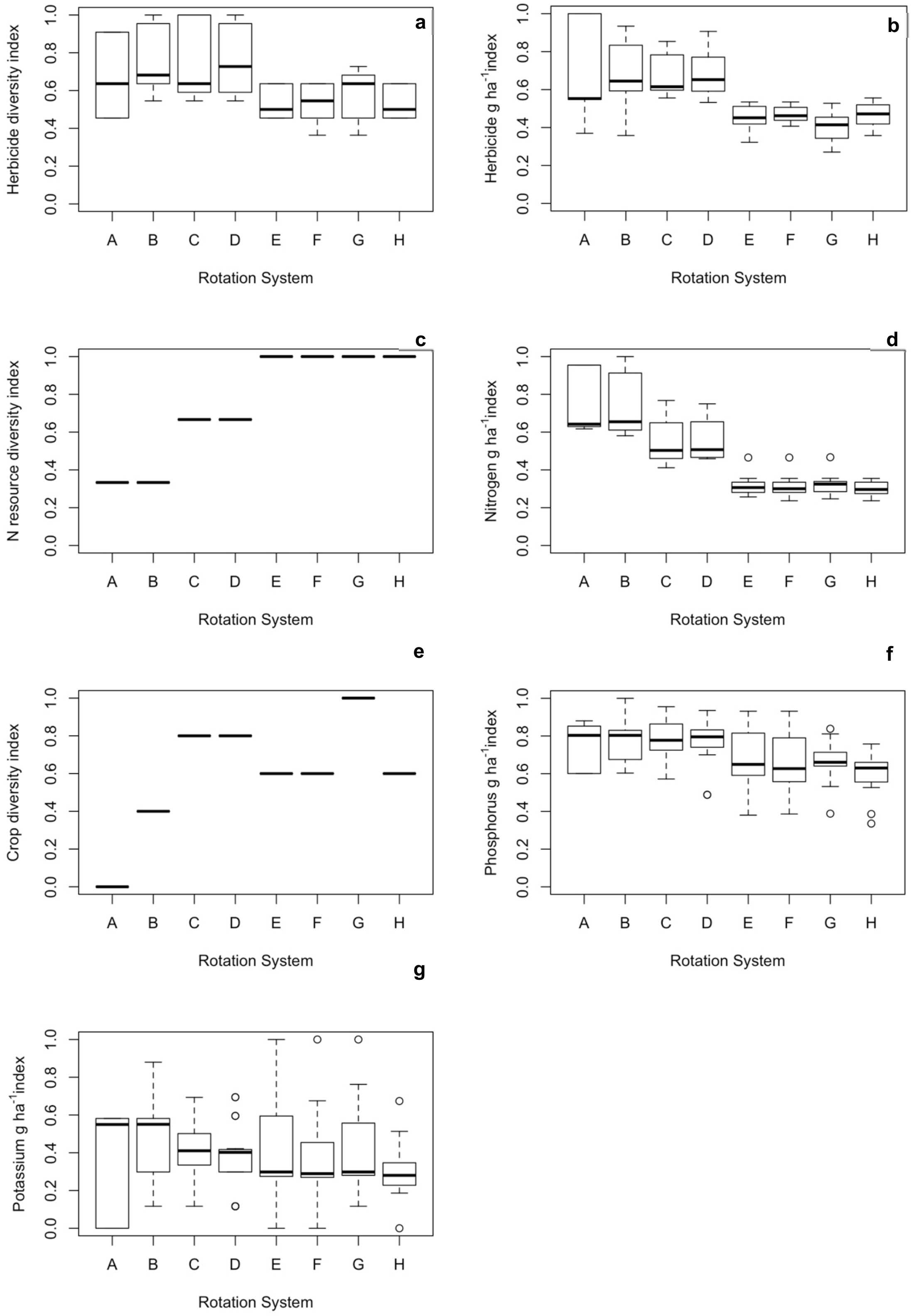
Weed community composition

A non-metric multidimensional scaling (NMS) ordination based on the Bray-Curtis distance measure was employed to explore variation in weed community composition between each plot in each period. An NMS is an unconstrained ordination technique, and was chosen over a constrained ordination approach as constrained ordinations are based on linear regression, and would thus have been unreliable due to the collinearity among management variables.

Table 4.2: A description of the indices of management and resource variables investigated in relation to weed abundance and diversity. All indices have been scaled to between 0 and 1 to make the model effect estimates comparable; this was done by expressing each value of each index as a proportion of the maximum value.

Variable	**Description**
Crop sequence diversity	The number of non-wheat years multiplied by the number of non-wheat crop types in each rotation system.
Herbicide AI (g ha^{-1})	The amount of active ingredient (AI) (g ha^{-1}) applied to each plot within each four-year period (standardised by active ingredient)
Herbicide diversity	The number of different herbicide mode-of-action applied to each plot within each four-year period
N / P / K (kg ha^{-1})	The total amount of fertiliser (kg ha^{-1}) applied to each plot within each four-year period. Separate indices were calculated for nitrogen (N), phosphorus (P) and potassium (K).
Nitrogen source diversity	The number of different types of nitrogen resource (nitrogen fertiliser, legumes, and sheep manure/urine) available within each rotation system
Grazed/ungrazed	Whether the rotation system included sheep forage phases or not (all systems with sheep had two forage phases).

Figure 4.2: Variation in management and resource indices among rotation systems for all plots in each period: (a) herbicide active ingredient (AI, g ha^{-1}), (b) herbicide diversity, (c) crop diversity index, (d) nitrogen resource diversity, (e) nitrogen fertiliser (kg ha^{-1}), (e) phosphorus fertiliser (kg ha^{-1}), and (g) potassium fertiliser (kg ha^{-1}). Box plots indicate the median, interquartile range, and minimum and maximum (open circles are points more 1.5 times the interquartile range from the median).



4.4 Results

Weed diversity and abundance and wheat yield in different rotations

Rotation system had a significant effect on all three responses investigated: weed abundance, weed diversity and relative wheat yield (Table 4.3). Pairwise comparisons indicated that all rotations containing grazed forage phases (E-H) had significantly lower weed abundances and higher weed diversity than ungrazed rotations (Figure 4.3). The shorter grazing duration in system H did not have an effect, as weed abundance and diversity in system H were not significantly different from that of systems E or F. System G, the grazed rotation with the highest crop diversity, had a significantly lower weed abundance and higher weed diversity than all other rotation systems, excluding E. However, the pairwise comparisons did not otherwise indicate that more diverse rotations had lower weed abundance or higher weed diversity than less diverse rotations, within either the non-grazed (A-D) nor grazed systems (E-F).

Table 4.3: Fixed effect estimates and P-values from the models of weed abundance, weed diversity and relative wheat yield in response to rotation system and time period (see also Figure 4.3). Time period was not included in the yield model (variation over time was accounted for by using yield standardised within each year). Estimates for Periods 2 and 3 and relative to Period 1. The model estimates for the interaction between each level of period and rotation are not shown, as the interaction was not significant (NS).

	Abundance		**Diversity**		**Wheat yield**	
	Estimate	P-value	Estimate	P-value	Estimate	P-value
System B	1.47	<0.001	-0.45	<0.001	-0.17	0.027
System C	1.1		-0.3		-0.07	
System D	0.92		-0.23		0.05	
System E	0.82		-0.19		0.04	
System F	-1.03		0.42		0.03	
System G	-0.72		-0.06		-0.03	
System H	-2.01		0.77		0.08	
Period 2	-0.22	0.033	-0.03	0.654	-	-
Period 3	0.04		-0.02			
Interaction (rotation x period)	NS	0.155	NS	0.138	-	-

Weed abundance was also significantly affected by time period, and increased slightly from Period 1 to Period 3 (Figure 4.3b); this may have been in response to rainfall differences between periods, or may indicate evolution of herbicide resistance amongst weed populations. For relative wheat yield, the monoculture wheat system A had a significantly lower yield than the four most diverse rotations (C, D, G, and H), and there was a general trend that wheat yields increased with crop diversity (Figure 4.3). Absolute wheat yields (not standardised within each year) were also explored for any obvious trends over time, but the inter-annual variation in response to rainfall was too great to identify any trends in absolute yields (results not shown).

Weed diversity and abundance in relation to management and resource diversity and intensity/availability

Of all the management and resource indices, only crop diversity had a significant main effect on weed abundance and weed diversity (Table 4.4). However, grazing, herbicide amount, nitrogen availability and nitrogen source diversity all had significant interactions with crop diversity (Table 4.4). The lack of a significant main effect may be due to the experimental design in relation to the variables tested. For example, there were no grazed systems at low crop diversities, and thus the model had no information with which to estimate an effect of grazing in the absence of crop diversity. The significant interaction indicates that grazing affected the relationships between crop diversity and weed abundance and diversity: Figure 4.4 illustrates that as crop diversity increases, weed abundance decreases; but if the rotation system contains sheep, then weed abundance decreases further for a given increase in crop diversity (Table 4.4; Figure 4.4, Figs 5a and 5b). The same trend exists for herbicide amount, nitrogen source diversity and nitrogen availability. Herbicide group diversity, and phosphorus and potassium fertiliser availability, were not significantly associated with either weed abundance or diversity (results not shown). Overall, the model results indicate that higher weed abundances and lower weed diversity occurred in ungrazed rotations and were associated with decreased crop diversity, increased quantities of herbicides and higher maximum nitrogen availability, and reduced nitrogen source diversity (Table 4.4, Figure 4.4, Figure 4.5). The individual contribution of each variable to the variance in weed abundance and diversity could not be attributed, given the collinearity between them. However, the AIC is lowest for the model containing crop diversity and grazing (Table 4.4), suggesting that these are the strongest drivers of differences in weed abundance and diversity.

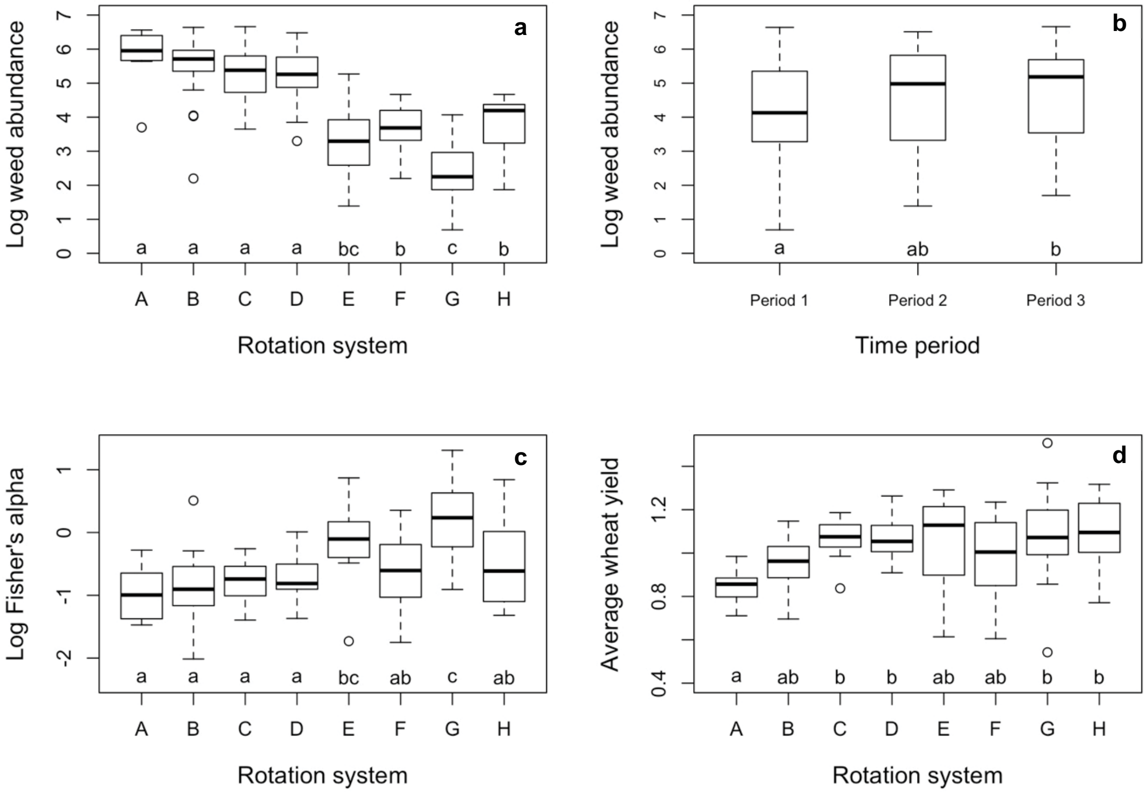


Figure 4.3: Relationships between weed abundance, weed diversity, wheat yield and rotation system and time period: (a) log weed abundance in the different rotation systems; (b) log weed abundance in the different time periods; (c) Fisher's log series alpha diversity index of weeds in the different rotation systems; (d) relative wheat yield in the different rotations. Categories with significant pairwise differences ($P<0.05$) do not share letters along the base of the plot. Refer to Table 4.1 for rotation system crop sequences, and to Table 4.3 for model statistics.

Time period had a significant effect in some models, although the effects were small compared with the effects of the management and resource variables. The models suggest either a small decrease or increase in weed abundance in period 2 from period 1, then a larger increase in period 3 (see also Figure 4.3b). Both periods were typically associated with a small decline in diversity, although this was significant only in the model including the total N fertiliser index. Rainfall also increased in Period 3, possibly explaining this trend (results not shown).

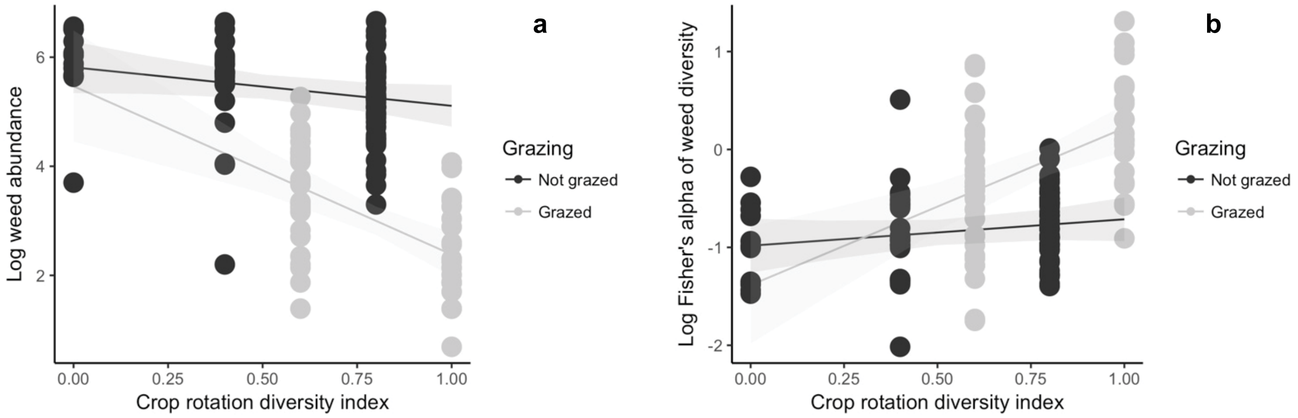


Figure 4.4: The relationship between weed abundance (a) and weed diversity (b), for grazed (dark shading) and non-grazed (light shading) rotation systems. The lines and ribbons indicate the regression coefficient and 95% confidence interval. This illustrates the interaction between grazing and crop diversity: the effect of crop diversity is greater in grazed than ungrazed systems.

Weed community composition in relation to rotation system, time period, management and resource indices

Ten weed species emerged from the seedbank samples over the twelve years (Table 4.5), excluding volunteer crop seedlings and the occasional unidentifiable seedling. *Lolium* spp., (a hybrid complex primarily between *L. rigidum* and *L. perenne;* Ferreira et al 2001) was by far the most dominant weed in the system: on average 77% of seedlings in each sample were *Lolium* seedlings (Table 4.5).

Table 4.4: The results of the linear mixed models for each index of filter strength or diversity (Table 4.2). Results for weed abundance are shown in the left column and for weed diversity in the right, with values given for the fixed effect estimates (random effects not shown) and the P-values calculated by parametric bootstrapping. The Akaike Information Criteria (AIC) is given to compare the goodness-of-fit of models for the different indices, and should be compared amongst abundance models and amongst diversity models, not between the two.

	Abundance		**Diversity**	
	Estimate	P-value	Estimate	P-value
Model: herbicide AI (g ha^{-1})				
Herbicide total AI (g ha^{-1}) index	0.40	0.676	-0.53	0.335
Crop diversity	**-5.37**	**<0.001**	**1.72**	**0.001**
Interaction (crop div x HX ha^{-1})	**6.01**	**<0.001**	**-1.86**	**0.019**
Period 2	**-0.13**	**0.006**	**-0.06**	**0.019**
Period 3	**0.33**		**-0.13**	
AIC	*396.9*		*222.2*	
Model: grazing				
Grazed	0.17	0.548	0.2	0.228
Crop diversity	**-1.9**	**<0.001**	**0.94**	**<0.001**
Interactions (crop div x sheep)	**1.19**	**0.003**	**-0.67**	**0.005**
Period 2	**-0.27**	**0.005**	0	0.916
Period 3	**0.08**		-0.02	
AIC	*353.6*		*217.2*	
Model: N fertiliser (kg ha^{-1})				
N fertiliser (kg ha^{-1}) index	0.06	0.949	0.32	0.610
Crop diversity	**-5.51**	**<0.001**	**2.05**	**<0.001**
Interaction (crop dix x N fertiliser)	**8.6**	**<0.001**	**-2.88**	**0.004**
Period 2	**0.01**	**0.002**	**-0.08**	**0.058**
Period 3	**0.34**		**-0.09**	
AIC	*373.4*		*226.4*	
Model: N source diversity				
N source index	0.31	0.756	-0.84	0.120
Crop diversity	**4.38**	**<0.001**	**-1.53**	**0.007**
Interaction (crop div x N sources)	**-7.35**	**<0.001**	**3.01**	**<0.001**
Period 2	**-0.27**	**0.006**	0	0.910
Period 3	**0.08**		-0.02	
AIC	*369.1*		*221.9*	

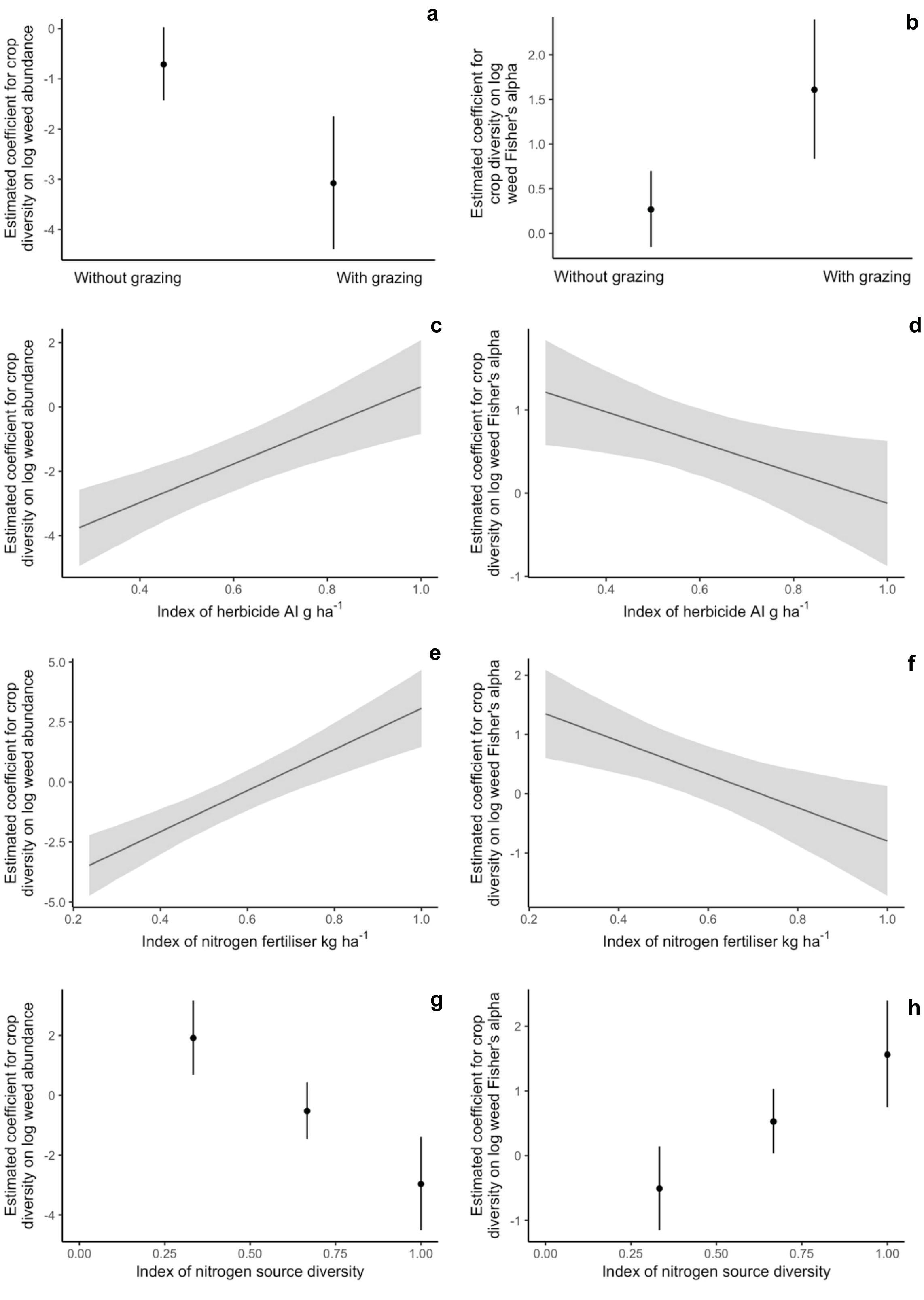

a
Estimated coefficient for crop diversity on log weed abundance
0
-1
-2
-3
-4
Without grazing
With grazing
b
Estimated coefficient for crop diversity on log weed Fisher's alpha
2.0
1.5
1.0
0.5
0.0
Without grazing
With grazing
c
Estimated coefficient for crop diversity on log weed abundance
2
0
-2
-4
0.4
0.6
0.8
1.0
Index of herbicide AI g ha^{-1}
d
Estimated coefficient for crop diversity on log weed Fisher's alpha
1
0
-1
0.4
0.6
0.8
1.0
Index of herbicide AI g ha^{-1}
e
Estimated coefficient for crop diversity on log weed abundance
5.0
2.5
0.0
-2.5
-5.0
0.2
0.4
0.6
0.8
1.0
Index of nitrogen fertiliser kg ha^{-1}
f
Estimated coefficient for crop diversity on log weed Fisher's alpha
2
1
0
-1
0.2
0.4
0.6
0.8
1.0
Index of nitrogen fertiliser kg ha^{-1}
g
Estimated coefficient for crop diversity on log weed abundance
2
0
-2
-4
0.00
0.25
0.50
0.75
1.00
Index of nitrogen source diversity
h
Estimated coefficient for crop diversity on log weed Fisher's alpha
2
1
0
-1
0.00
0.25
0.50
0.75
1.00
Index of nitrogen source diversity

Figure 4.5: Interaction plots showing the change in the effect of crop diversity on weed abundance and diversity between grazed and ungrazed systems (a and b), as the amount of herbicide applied increased (c and d), nitrogen fertiliser applied increase (e and f) and the diversity of nitrogen sources increased (g and h). These interactions result in the relationships between crop diversity and weeds illustrated in Figure 4.4: grazed systems had lower amounts of herbicide applied, less fertiliser applied and higher nitrogen source diversity than non-grazed systems (Figure 4.2, Table 4.4).

Table 4.5: Species observed to emerge in the seedbank samples from the Langgewens Long-Term Trial over the 12 years from 2005 to 2016, and the average proportion of abundance of each species across all plots in all periods of the trial. *Lolium* spp. could not be identified to species level due to hybridisation.

Code	**Latin name**	**Afrikaans name**	**English name**	**Status**	**Average proportion of abundance across all plots in all periods**
acal	*Arctotheca calendula*	gousblom	capeweed	native	<0.01
bdia	*Bromus diandrus*	predikantluis	ripgut brome	alien	<0.01
calb	*Chenopodium album*	wit hondebossie	fat hen	alien	<0.01
cot	*Cotula* spp.	gansogie	goose-eyes	both	0.04
eaus	*Emex australis*	dubbeltjie	devil’s thorn	alien	<0.01
emos	*Erodium moschatum*	turknaal	musk heron's bill	alien	0.04
lol	*Lolium* spp.	raaigras	ryegrass	alien	0.77
mpar	*Malva parviflora*	kiesieblaar	mallow	alien	0.03
pavi	*Polygonum aviculare*	litjiesgras	knotweed	alien	0.09
rrap	*Raphanus raphanistrum*	ramenas	wild radish	alien	<0.01

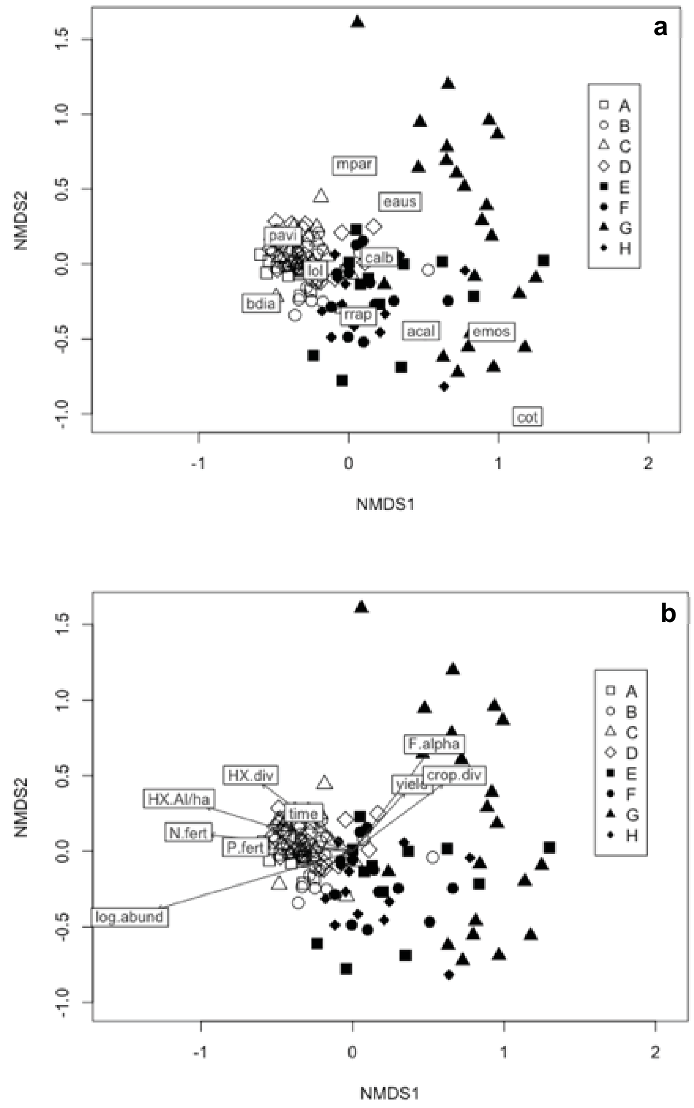


Figure 4.6: Two-dimensional non-metric multidimensional scaling ordination of the weed communities of each plot in each period. Symbols indicate plots belonging to the different rotation systems; shaded symbols are grazed systems. Labels on (a) represent the species associated with samples in different parts of the ordination, based on weighted averages (see Table 4.5 for species abbreviations). Arrows on figure (b) represent significant correlations (P<0.05) between variation in community composition and management and resource indices (Table 4.2), as well as weed abundance (“log.abund”), Fisher’s alpha diversity (“F.alpha”) and wheat yield (“yield”). The length of the arrows is relative to the strength of the correlation. Time is plotted as a continuous variable: change between periods was significant, but the direction of change sufficiently small that plotting periods as category centroids is confusing to the eye.

A two-dimensional NMS solution was selected to represent variation in the relative frequency of these species across the trial. Two dimensions reduced stress to an acceptable level (ordination stress = 0.17 and non-linear $R^2 = 0.97$), and whilst the addition of a third dimension reduced stress further (to 0.12), it did not alter any trends shown, and was thus omitted to conserve interpretability. The ordination indicates that ungrazed systems were associated with consistently high abundances of *Polygonum aviculare* and *Lolium* spp., while species composition varied more within grazed systems (Figure 4.6a). It also illustrates the association between grazed rotations and reduced weed abundance, increased weed diversity, and increased wheat yields (Figure 4.6b).

4.5 Discussion

In this trial, diverse cropping systems with integrated livestock offered the best outcomes for farm productivity and environmental protection: fewer agrichemicals were applied, weed abundance was lower, weed diversity was higher, and wheat yields were higher. The greatest differences in weed management were between grazed systems (E-H) and ungrazed systems (A-D), but crop sequence diversity also contributed. Overall, the most diverse grazed system (G) performed best, while the wheat monoculture (system A) performed worst. The results of the models of management and resource indices further support that grazing and crop diversity are the strongest drivers of weed abundance and diversity within this trial (Table 4.4, Figure 4.4, Figure 4.5).

The strong impact of grazing on weeds supports our first hypothesis that the diversity of management filters, in particular disturbance diversity, can suppress weed abundance and promote weed diversity. Introducing a grazed phase to a rotation adds a disturbance with a distinct selection pressure from herbicides, which may explain why grazing was found to have an impact on weed abundance and diversity, but herbicide group diversity was not (Table 4.4). Although different herbicides target different species, all herbicides would impose selection pressure for traits that permit general herbicide tolerance of avoidance (such as lower leaf permeability, variable germination times or early maturity; Gaba et al 2017). In contrast, grazing selects for traits that confer unpalatability or resilience to physical defoliation. This suggests that maximising differences in selection pressure between management filters results in more effective weed management.

Findings from other studies on integrated crop-livestock systems support this conclusion that it is filter diversity, rather than grazing in itself, that offers the greatest benefits for weed management. For example, Miller et al (2015) found that replacing herbicide-based or tillage-based management of a forage crop with grazing did not consistently improve weed suppression, while Lehnhoff et al (2017) show that grazing can reduce reliance on tillage in organic systems but not completely eliminate the need for it. Thus, it is combining distinct selection pressures that is most effective to suppress weeds. Where integrating forage crops and livestock is not practical for farmers, incorporating a mown cover crop may have similar benefits through exerting a similar filter on weeds (McKenzie et al 2016), except in cases where problematic weed species are particularly susceptible to grazing (Leon and Wright 2018).

In this study, the greater dominance of *Lolium* spp. and *P. aviculare* in crop-only systems (Figure 4.6) illustrates the effect of the contrasting selection pressures between herbicides and grazing, and the specific effects of grazing on susceptible weeds. Both weeds possess traits conferring herbicide tolerance but both are palatable to sheep. As such, *Lolium* spp. and *P. aviculare* could be viewed as additional forage species promoted by cash crop phases, and the grazing phases as an important strategy for managing these weeds, particularly for any herbicide resistant populations. Resistant *Lolium* is a widespread problem in the Western Cape, and although it is not known whether *Lolium* present in the trial was resistant, this could explain the dramatic differences in weed abundance between the grazed and ungrazed systems. It remains uncertain whether mowing would have similar benefits in these systems.

Previous long-term studies that included two weed control measures with different selection pressures, such as herbicides and tillage, have often not observed reductions in weed biomass when compared with chemical control only (e.g. Chikowo et al 2009, Benaragama et al 2016). However, in such studies, both management actions are typically applied in every year, regardless of crop type. This would create a stronger filter for weed species that can tolerate both management actions, rather than enhancing filter diversity by selecting for tillage-tolerant weeds in one year and herbicide-tolerant weeds in another. In contrast, trials involving more inter-annual variation in management appear to achieve better weed outcomes (Blackshaw et al 2008, Davis et al 2012, Anderson 2015). In this study, management in the grazed systems varied between high herbicide use in cash crop years, and low herbicide use with grazing in forage crop years. Varying selection pressures between years may therefore be key to successful integrated weed management, although this has yet to be explicitly tested.

In addition to higher filter diversity, the grazed systems in this study also had less herbicide applied (lower disturbance strength), less nitrogen fertiliser applied (lower maximum resource availability), and a higher nitrogen source diversity than ungrazed systems (Figure 4.2). From an applied perspective, this provides evidence that integrating livestock permits weeds to be suppressed and yields to be maintained at lower levels of agrichemical inputs, offering both environmental and economic benefits (Petit et al 2015, Basson 2017). However, from a theoretical perspective, this collinearity makes it difficult to distinguish the relative roles of the mechanisms identified in our hypotheses: the effect of disturbance diversity induced by grazing may have been further enhanced by these other attributes of grazed systems (Storkey et al 2010, Smith et al 2010, Gaba et al 2013, Reich 2014).

The effect of crop diversity on weed abundance and diversity in this study was smaller than that of grazing (Figure 4.3, Figure 4.4), but still important, given that other management variables were significant only in interaction with crop diversity (Table 4.4, Figure 4.5). Crop diversity could affect the weed community through variation in filters imposed by competition, as different crops compete more strongly with certain weeds than others (Petit et al 2015, Nichols et al 2015). Differences in the timing of crop sowing often play a role in determining which weed species emerge, but in this trial all crops were sown at the same time. Several other studies on weed responses to crop rotation have found little or no effect of crop diversity independent of management diversity (Smith and Gross 2007), but the functional differences between the crops in this study were relatively large, and thus may have had a greater effect on weeds.

In contrast to weed abundance and diversity, average wheat yields were more strongly related to crop sequence diversity than to grazing, and were highest in the four most diverse systems (C, D, G and H). Crop diversity contributes to yield in several ways, for example through increasing soil nutrient content and reducing disease, and such effects may be more important to yield than weed suppression (Davis et al 2012, Benaragama et al 2016). The main advantage of integrating livestock into rotation systems is thus not necessarily to improve crop yields, but to decrease the amount of herbicide required for satisfactory weed management. A separate study investigating the economics of the rotation systems in the Langgewens Long-Term Trial found that although yields were comparable between diverse grazed and ungrazed systems, the reduced cost of inputs and increased diversity of marketable outputs in grazed rotations resulted in higher long-term farm profits (Basson 2017).

This study emphasises the benefits that diverse cropping systems with integrated livestock can offer to farmers, agroecosystems, and the natural environment (Davis et al 2012, Sanderson et al 2015). Forage crops provide an opportunity to increase crop diversity, which benefits cash crop yields and reduces fertiliser requirements, while the grazing action of livestock improves weed management and facilitates reductions in herbicide use. Integrating livestock forage phases may therefore prove valuable to sustain arable crop production in the face of herbicide resistance, and to reduce the risks associated with intensive agrichemical use, particularly in no-till systems where non-chemical weed management options are limited. Likewise, there may be potential to improve weed management in organic and low-input cropping systems using grazed forage phases to provide an additional filter alongside mechanical weeding and tillage. Future research could focus on how management actions that apply different selection pressures to weeds can best be integrated in rotation systems, to allow farmers to optimise the use of the weed management tools that are available to them.

4.6 Acknowledgements

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4.7 Author contributions

J. Strauss manages the Langgewens Long-Term Trial and oversaw all data collection for this study. C.M., J. Storkey and K.D. planned how to analyse the data to answer the questions posed in this article, and C.M. undertook the data analysis with support from J. Storkey. CM drafted the manuscript with advice from P.S. and K.D. All authors contributed critical revisions to the manuscript.

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4.9 Appendix

A schematic of the design of the Langgewens Long-Term Trial. The schematic is not representative of the spatial layout (a randomised block layout) but illustrates the replication of the systems and crop types. Each system is replicated twice, and within each replicate, each crop sequence is replicated at least once. Systems A, E, F and H contain fewer plots per replicate because they contain fewer sequences; for example, A only contains ‘wheat after wheat’ and E only contains ‘wheat after medic’ and ‘medic after wheat’. In contrast, system C has ‘wheat after canola’, ‘wheat after lupin’, ‘canola after wheat’ and ‘lupin after wheat’, which are all represented in each replication in each year. These sequences were not relevant to this study due to aggregating the data within each four-year period, but are relevant to some of the other ongoing agronomic studies within the trial. Within the schematic, grazed crop types are indicated by an asterisk (*).

System	Replicate	Plot	Year 1	Year 2	Year 3	Year 4
A	Rep 1	1	wheat	wheat	wheat	wheat
		2	wheat	wheat	wheat	wheat
	Rep 2	1	wheat	wheat	wheat	wheat
		2	wheat	wheat	wheat	wheat
B	Rep 1	1	wheat	wheat	wheat	canola
		2	wheat	wheat	canola	wheat
		3	wheat	canola	wheat	wheat
		4	canola	wheat	wheat	wheat
	Rep 2	1	wheat	wheat	wheat	canola
		2	wheat	wheat	canola	wheat
		3	wheat	canola	wheat	wheat
		4	canola	wheat	wheat	wheat
C	Rep 1	1	wheat	canola	wheat	lupin
		2	canola	wheat	lupin	wheat
		3	wheat	lupin	wheat	canola
		4	lupin	wheat	canola	wheat
	Rep 2	1	wheat	canola	wheat	lupin
		2	canola	wheat	lupin	wheat
		3	wheat	lupin	wheat	canola
		4	lupin	wheat	canola	wheat
D	Rep 1	1	wheat	wheat	lupin	canola
		2	wheat	lupin	canola	wheat
		3	lupin	canola	wheat	wheat
		4	canola	wheat	wheat	lupin
	Rep 2	1	wheat	wheat	lupin	canola
		2	wheat	lupin	canola	wheat
		3	lupin	canola	wheat	wheat
		4	canola	wheat	wheat	lupin
E	Rep 1	1	wheat	medic*	wheat	medic*
		2	medic*	wheat	medic*	wheat
	Rep 2	1	wheat	medic*	wheat	medic*
		2	medic*	wheat	medic*	wheat
F	Rep 1	1	wheat	medic/clover*	wheat	medic/clover*
		2	medic/clover*	wheat	medic/clover*	wheat
	Rep 2	1	wheat	medic/clover*	wheat	medic/clover*
		2	medic/clover*	wheat	medic/clover*	wheat
G	Rep 1	1	medic*	wheat	medic*	canola
		2	wheat	medic*	canola	medic*
		3	medic*	canola	medic*	wheat
		4	canola	medic*	wheat	medic*
	Rep 2	1	medic*	wheat	medic*	canola
		2	wheat	medic*	canola	medic*
		3	medic*	canola	medic*	wheat
		4	canola	medic*	wheat	medic*
H	Rep 1	1	wheat	medic/clover*	wheat	medic/clover*
		2	medic/clover*	wheat	medic/clover*	wheat
	Rep 2	1	wheat	medic/clover*	wheat	medic/clover*
		2	medic/clover*	wheat	medic/clover*	wheat

CHAPTER 5: COVER CROP MIX COMPOSITION IS MORE IMPORTANT THAN MIX DIVERSITY FOR WEED SUPPRESSION

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5.1 Abstract

Diverse cover crop mixes are popular to achieve multiple goals simultaneously. The biotic resistance theory suggests that a diverse mix may also be specifically effective for weed suppression: diversity may increase resource capture through niche differentiation, thus reducing resource availability to weeds. To investigate, we designed eight cover crop mixes that varied in species diversity, functional diversity, and composition. Mixes contained either one, four or eight species, in equal proportions. Three mixes contained only cereal species, three contained only legumes, and two contained a mix of cereals, legumes and brassicas. Mixes were sown in 84 m^2 plots in a randomised complete blocked design on two farms in South Africa's winter rainfall region, replicated over two years. Indicators of resource uptake by each mix in terms of light, soil nitrogen and water were measured at three time points throughout the season, approx. 50, 85 and 110 days after establishment (DAE). Dry weight of cover crops and weeds within each mix was measured twice, at approximately 70 and 120 DAE. Regression analyses indicated that cover crop biomass was key to resource uptake and weed suppression, and that early-season nitrogen and later-season light availability had the strongest influence on weed biomass. Neither species nor functional diversity affected resource uptake or weed suppression by cover crops. These results indicate that it is important to consider the competitiveness of individual species when designing cover crop mixes. Diverse mixes remain valuable for multifunctionality, but may contribute to weed problems if composed of poorly competitive species.

5.2 Introduction

Cover crops, defined as crops planted for a purpose other than harvest, are integrated into cropping systems to achieve a variety of goals. Cover crops can be used to conserve and improve soil quality, provide resources to biodiversity, break pest and disease cycles, and suppress weeds (Snapp et al 2005, Blanco-Canqui et al 2015). Recently, cover crops comprising mixes of different species have become popular, as combining species with different properties creates a single crop that can perform multiple functions (Storkey et al 2015, Finney et al 2017). Combining multiple species may also increase the capacity of a cover crop to perform individual functions. This concept has not yet been extensively tested in cover crops, and there is mixed evidence so far (e.g. Döring et al 2012a, Finney et al 2016). However, in general, increased plant diversity is known to be associated with increased provision of several specific ecosystem functions (Isbell et al 2017), including productivity (Tilman et al 2012), soil carbon storage (Lange et al 2015), nutrient cycling (Oelmann et al 2011) and the support of further biodiversity (Scherber et al 2010). Diversity is thought to increase the magnitude and resilience of an ecosystem function because each species performs the function in a different way, or at different rates under different conditions, leading to a higher overall capacity to consistently perform the function (Díaz and Cabido 2001, Isbell et al 2011). Functional diversity (the value and range of those species and organismal traits that influence ecosystem functioning; Tilman 2001) is considered to have a stronger effect on ecosystem functioning compared with species diversity. Functionally different species are more likely to have distinct strategies (distinct niches) to perform the function, and thus their strategies are more likely to be complementary rather than overlapping, and thus lead to greater functioning (Díaz and Cabido 2001).

One function of cover crops that has potential to be improved by increased diversity is weed suppression. Cover crops primarily suppress weeds by competing with them for resources (although allelopathy can also play a role; Blanco-Canqui et al 2015). Thus, combining different species that acquire resources from their surrounding environment in different ways could result in increased overall resource capture, so that fewer resources would remain available to weeds than if a monoculture cover crop was used. This concept has been explored in invasion ecology, where it was first put forward by Elton (1958) and forms a central pillar of the ‘biotic resistance’ or ‘diversity-invasibility’ hypothesis (Richardson and Pyšek 2006, Jeschke 2014). Biotic resistance can be defined as a resident community’s capacity to resist invasion by alien species, and in the context of plant communities, diversity may contribute in two ways (Shea and Chesson 2002, Funk et al 2008). First, according to the niche differentiation hypothesis, the additive effect of each species acquiring resources in different ways could result in more efficient overall resource capture. Second, the sampling effect hypothesis states that a diverse community would be more likely to contain a few species that are particularly effective at resource capture, thereby lowering overall resource availability and reducing opportunities for invasion. The sampling effect may also manifest as an increased likelihood of limiting similarity, where the community contains species that use resources in similar a fashion to the invader, and these species are thus more likely to suppress the invader through competitive exclusion (limiting similarity) (Funk et al 2008).

Empirical support for a positive relationship between species diversity and biotic resistance via either niche differentiation, limiting similarity and/or the sampling effect has been inconsistent (Levine and D’Antonio 1999, Jeschke 2014). The current consensus in the literature is that diversity can play a role, but its effect is often obscured by other variables such as abiotic disturbance and fluctuating resource availability (Richardson and Pyšek 2006). Several authors have noted a scale-dependent pattern, where resident diversity increases biotic resistance at small spatial and temporal scales, but at landscapes scales and over decades resident diversity is often the result of high resource availability and frequent resource fluctuations, conditions that also promote invasion by alien species (Levine 2000, Nunez-Mir et al 2017). However, the findings that diversity can increase resistance at small scales suggests that the principle could be applied to increase cover crop suppression of weeds at the scale of a farm field.

Few studies so far have investigated the relationship between the diversity of cover crop mixes and their capacity for weed suppression, and their findings have been inconsistent. Some previous studies suggest functional diversity may increase weed suppression (Linares et al 2008, Döring et al 2012a), while others suggest that the biomass produced by a cover crop is the main predictor of weed suppression, and that diversity does not play a role (Brennen and Smith 2005, Smith et al 2014, Smith et al 2015, Finney et al 2016). These latter studies suggest that whilst the sampling effect may play a role in natural systems by increasing the chances that a particularly competitive species will be present, in agricultural systems we could simply choose to sow the most competitive species, or pick the species most likely to suppress locally abundant weeds through limiting similarity.

Another potential role of cover crop diversity in weed management is that diverse cover crops may help to promote a more beneficial weed community. Although weeds are considered primarily detrimental to crop production, weeds can benefit agroecosystem functioning by supporting other beneficial organisms (Petit et al 2011), and the provision of this service is expected to be higher when the weed community is more diverse (in this context, a low abundance of diverse weeds could perhaps be considered an unplanned but nonetheless beneficial component of a cover crop). A study by Palmer and Maurer (1997) indicated that diverse cover crop mixtures may promote weed diversity, possibly through the creation of diverse microhabitats and/or by combining different crops that promote or facilitate different groups of weeds. However, a more recent trial by Smith et al (2015) found no evidence for such a relationship.

Overall, there is a promising theoretical basis that increasing cover crop diversity could improve management, but inconsistent results from previous studies indicate a need for further experimental evidence. To investigate how cover crop diversity influences weed abundance and community composition, this paper presents a field trial designed to systematically test the effects of different levels of both species diversity and functional diversity on weeds, and to investigate whether any effect can be explained by increased resource capture. Specifically, we test the following hypotheses:

(A) increased cover crop species diversity and/or increased cover crop functional diversity increases weed suppression;

(B) the capacity of a cover crop mix to suppress weeds can be explained by its ability to capture resources;

(C) specific cover crop functional types are more effective at suppressing weeds of comparable functional types;

(D) a more diverse cover crop mixture promotes a more diverse weed community.

(E) cover crops that are more effective in weed suppression result in higher cash crop yields in the following year.

5.3 Methods

Trial overview, location and layout

To test our four hypotheses, we designed a field experiment consisting of cover crop mixes that differed in species diversity, functional diversity, and the functional types of species included in the mix. We assessed the effect of each mix on overall weed biomass, and identified whether the species diversity, functional diversity, composition or biomass of each cover crop mix best explained the effect on weed biomass (hypothesis A). To understand whether these cover crop mix characteristics influenced weed biomass through reducing resource availability to weeds, we explored how cover crop characteristics related to the availability of light, moisture and nitrogen throughout the season, and also investigated whether or not weed biomass responded to the availability of these resources (hypothesis B). To assess whether limiting similarity played a role (hypothesis C) we explored whether different cover crop functional types reduced the biomass of weeds of similar functional types to a greater degree. We also investigated whether weed species diversity increases as cover crop diversity increases (hypothesis D). Lastly, to assess the agronomic significance of the cover crop mixes, we explored how the different cover crop mixes and their ability to suppress weeds was linked to cash crop yields in the following year (hypothesis E).

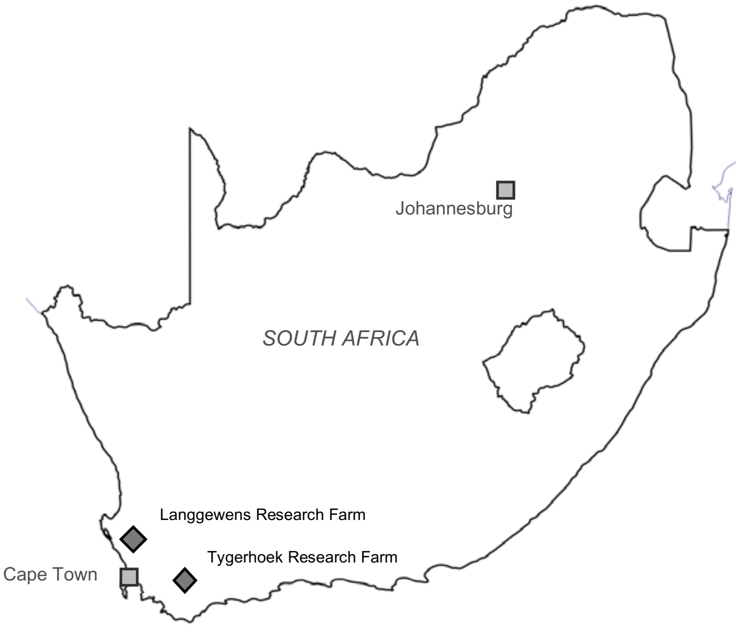

Figure 5.1: The location of Langgewens and Tygerhoek Research Farms in South Africa.

The different cover crop mixes were trialled on two farms in South Africa's Western Cape winter rainfall region, Langgewens and Tygerhoek Research Farms (Figure 5.1) of the Western Cape Government Department of Agriculture. Langgewens receives an average annual rainfall of 408 mm (SD = 109 mm) of which approximately 80% falls between April and September. Tygerhoek receives an average annual rainfall of 511 mm (SD = 101 mm) with approximately 60% falling between April and September. The dominant weed at both sites is Lolium spp., thought to be a hybrid complex of L. rigidum, L. multiflorum and L. perenne (Ferreira et al 2013). These research farms are representative of field cropping systems in the region, where most farms follow conservation agriculture practices, including no-tillage or minimum-tillage, crop rotation, and crop residue retention, and where the main crops are winter cereals, canola (Brassica napus), and legume forages. Due to the annual rainfall distribution, only one crop per year can be grown in the winter months, so a cover crop replaces a cash crop. Vineyards and orchards are also major cropping systems in the Western Cape winter rainfall region, and annual cover crops are used to protect soil and suppress weeds in winter. Findings from this trial are thus applicable to both annual field crop and perennial fruit and wine crop systems in the region.

The trial was laid out in randomised blocked design, with three blocks on each farm. Each treatment plot was 4.2 m wide by 20 m long. At Langgewens, the blocks were located on three separate fields that had been continuously cropped with wheat (*Triticum aestivum*) since 1996, and the trials were surrounded by wheat. At Tygerhoek, all blocks were located in a single field with a mixed cropping history and the field around the trial was left fallow. Cover crops were sown directly into the residue of the previous year's crop using a no-tillage double-disc planter (typical practice in conservation agriculture systems). At Tygerhoek, there was minimal crop residue but a substantial amount of residue from summer weeds, particularly from the knotweed *Polyganum aviculare*. In 2016, the trial at Tygerhoek was planted on 11 May and at Langgewens on 18 May; in 2017 Tygerhoek was planted on 3 May and Langgewens on 12 May. The first substantial rainfall of the season was unusually late at both farms in both years (late May in 2016 and early June in 2017), so the trials were planted into dry soil. In 2016, seedling emergence occurred approximately 15 days after planting, and in 2017 approximately 25 days after planting. At the end of the season (late September/early October), the cover crops were rolled using a roller-crimper to terminate their growth and prevent them from setting seed.

In 2017, cash crops were also planted into the cover crop plots of 2016, to investigate the effects of the mixes on subsequent yield, and whether any effects were linked to weed suppression during the cover crop year. At Langgewens the cash crop was wheat, and forage oats (*Avena sativa*) were used at Tygerhoek. The wheat grain at Langgewens was harvested on 6th November 2017 and oat biomass samples collected at Tygerhoek on 25th October 2017. The oat grain was not harvested at Tygerhoek as a forage cultivar was used, and thus the grain yield may not be reflective of growth conditions.

Species selection and mix composition

The nine treatments consisted of a weedy fallow or ‘bare ground’ (BG) control where no cover crops were planted, two monoculture controls (a single cereal, 1C; and a single legume, 1L), three four-species mixes (four cereals, 4C; four legumes, 4L; and a diverse mix, 4D), and three high richness mixes (cereals, HC; legumes, HL; and a diverse mix, HD) (Table 5.1). Treatments differed slightly between the two years of the trial. In the first year (2016), a total of 21 different species was used, and the HL and HD mixes contained 12 species each. In 2017, the number of species in the H mixes was reduced to eight: species that did not establish well in 2016 were excluded from the trial in 2017. In 2016 there were not enough cereal species available to include an HC mix, so this treatment was only implemented in 2017. The HC mix consisted two rye *(Secale cereale)* varieties, a spring variety and a stooling variety, in addition to six other cereal species (Table 5.1). These two varieties were suggested by local agronomists to vary in phenology and growth habit as much as two different cereal species.

The selection of species to include in the trial was informed by common practices in the Western Cape (the species used for the 1C and 1L mixes are typical cover crops) and on advice from local experts, including government agronomists and commercial seed suppliers. Sowing rates were also based on advice from local experts. To create the mixes, the recommended sowing rate was divided by the proportion of the mix made up by each species; for example, in a four species mix, each species was sown at 25% of its recommended sowing rate (Table 5.1).

The functional diversity investigated in this study was diversity in spatial resource capture strategy: the species included differed in their growth forms and root architectures. Although plants do not compete for space *per se,* plants compete for the resources within a space (Booth et al 2003), and thus a group of plants capable of more completely occupying the three-dimensional space around them would be expected to deplete resources more uniformly from that space and thus more effectively reduce resource availability to weeds. Specifically, diversity in growth form was expected to allow the cover crops to create a more complete canopy cover to restrict light availability to weeds, and diversity in root architecture to allow the cover crop to more effectively deplete the soil of moisture, nitrogen and other key nutrients (Figure 5.2).

Species were divided into the functional types of ‘cereal’, ‘legume’, ‘brassica’ and ‘other’. These four groups have different strategies to utilise the space around them, and thus different strategies to acquire resources from that space (Figure 5.2). All cereal species included in the trial had a tufted, upright growth form and fibrous roots. Most legumes had prostrate or spreading growth forms, with a taproot and spreading lateral roots (with the exception of lupins *(Lupinus angustifolius)*, included in 2016 only, which had a more upright growth form). The two brassica species (white mustard, *Sinapis alba,* and forage radish, *Raphanus sativa*) had upright growth forms and deep taproots, while the ‘other’ consisted of chicory *(Cichorium intybus)* in 2016 and flax *(Linum usitatissimum)* in 2017 (this substitution was made given the very poor establishment of chicory in 2016). Chicory forms a rosette with a deep taproot, while flax has a shallow root system and slender upright growth form. In accordance with limiting similarity, cover crops with specific growth forms and root architectures were expected to suppress weeds with similar growth forms and root architectures, given that they are more likely to compete for resources within the same space. Weeds were divided into functional types that corresponded with those of the cover crops: ‘grasses’ (similar root architecture and growth form to cereals), ‘short or prostrate herbs’ (similar to legumes), and ‘tall upright herbs’ (similar to brassicas).

Data collection

Cover crop and weed biomass, diversity and composition

Dry-weight biomass of both cover crops and weeds was sampled twice in each year of the trial, once at ‘mid-season’ approximately 65 days after emergence (DAE) and once at ‘end-season’ approximately 140 DAE (just prior to termination). A 0.5 m^2 biomass sample was cut from each plot, from two 0.25 m^2 sub-samples located a random number of paces from each end of the plot (placed either to the left or right to avoid cutting the same area in both sample events). To determine botanical composition, biomass was sorted into each species of cover crop and weed, then dried at 60˚C for at least 72 hours, then weighed.

For both cover crop and weed species diversity and functional diversity we used the Shannon index based on the biomass of each species. The Shannon index was used because it is relatively sensitive to the presence of rare species, and the weed community in the trial locations was largely dominated by *Lolium* spp. (Magurran 2003). Mix composition was determined by the biomass of the different functional types in each sample, for both weeds and cover crops.

Figure 5.2: An illustration of the functional types used in this study, and the expected effects of functionally diverse or similar multi-species mixes on spatial resource capture.

Table 5.1: Cover crop species included in each mix: their common name, species name, and the sowing rate used.

Mix	BG	1C	1L	4C	4L	4D
YEAR 1	none	Triticale (140kg ha^{-1}) *(x Triticosecale)*	Barrel medic (10 kg ha^{-1}) *(Medicago truncatula)*	Triticale (35kg ha^{-1}) *(Triticosecale)* Rye (12.5kg ha^{-1}) *(Secale cereale)* Barley (15kg ha^{-1}) *(Hordeum vulgare)* Forage oats (25kg ha^{-1}) *(Avena sativa)*	Barrel medic (2.5kg ha^{-1}) *(Medicago truncatula)* Burr medic (3.75kg ha^{-1}) *(Medicago polymorpha)* Persian clover (1.5kg ha^{-1}) *(Trifolium resupinatum)* Subterranean clover (3kg ha^{-1}) *(Trifolium subterraneum)*	Barrel medic (2.5kg ha^{-1}) *(Medicago truncatula)* White mustard (2.5kg ha^{-1}) *(Sinapis alba)* Subterranean clover (3kg ha^{-1}) *(Trifolium subterraneum)* Triticale (35kg ha^{-1}) *(x Triticosecale)*
YEAR 2	none	Triticale (140 kg ha^{-1}) *(x Triticosecale)*	Burr medic (15kg ha^{-1}) *(Medicago polymorpha)*	Forage oats (25kg ha^{-1}) *(Avena sativa)* Barley (15kg ha^{-1}) *(Hordeum vulgare)* Rye (12.5kg ha^{-1}) *(Secale cereale)* Triticale (35kg ha^{-1}) *(x Triticosecale)*	Burr medic (3.75kg ha^{-1}) *(Medicago polymorpha)* Barrel medic (2.5kg ha^{-1}) *(Medicago truncatula)* Field peas (30kg ha^{-1}) *(Pisum sativa)* Woolly vetch (7.5kg ha^{-1}) *(Vicia villosa)*	Burr medic (3.75kg ha^{-1}) *(Medicago polymorpha)* White mustard (2.5kg ha^{-1}) *(Sinapis alba)* Subterranean clover (3kg ha^{-1}) *(Trifolium subterraneum)* Triticale (35kg ha^{-1}) *(x Triticosecale)*

Mix	HC	HL	HD
YEAR 1	-	Burr medic (1.25kg ha^{-1}) *(Medicago polymorpha)* Barrel medic (0.8kg ha^{-1}) *(Medicago truncatula)* Serradella (3.6kg ha^{-1}) *(Ornithopus sativa)* Berseem clover (0.8kg ha^{-1}) *(Trifolium alexandrinum)* Crimson clover (1kg ha^{-1}) *(Trifolium incarnatum)* Balansa clover (0.6kg ha^{-1}) *(Trifolium michelianum)* Red clover (0.8kg ha^{-1}) *(Trifolium pratense)* White clover (0.8kg ha^{-1}) *(Trifolium repens)* Persian clover (0.5 kg ha^{-1}) *(Trifolium resupinatum)* Subterranean clover (1kg ha^{-1}) *(Trifolium subterraneum)* Arrowleaf clover (1.6 kg ha^{-1}) *(Trifolium vesiculsum)* Woolly vetch (2.1kg ha^{-1}) *(Vicia villosa)*	Forage oats (8.25kg ha^{-1}) *(Avena sativa)* Chicory (0.6kg ha^{-1}) *(Cichorium intybus)* Barley (5kg ha^{-1}) *(Hordeum vulgare)* Lupin (5.8kg ha^{-1}) *(Lupinus angustifolius)* Barrel medic (0.8kg ha^{-1}) *(Medicago truncatula)* Field peas (10kg ha^{-1}) *(Pisum sativa)* Forage radish (0.8kg ha^{-1}) *(Raphanus sativa)* White mustard (0.8kg ha^{-1}) *(Sinapis alba)* Crimson clover (1kg ha^{-1}) *(Trifolium incarnatum)* Subterranean clover (1kg ha^{-1}) *(Trifolium subterraneum)* Triticale (11.7kg ha^{-1}) *(x Triticosecale)* Woolly vetch (2.1kg ha^{-1}) *(Vicia villosa)*
YEAR 2	Red oats (10kg ha^{-1}) *(Avena byzantina)* Forage oats (12.5kg ha^{-1}) *(Avena sativa)* Saia oats (12.5kg ha^{-1}) *(Avena strigose)* Barley (7.5kg ha^{-1}) *(Hordeum vulgare)* Rye, spring (6.25kg ha^{-1}) *(Secale cereale)* Rye, stooling (7.5kg ha^{-1}) *(Secale cereale)* Triticale (17.5kg ha^{-1}) *(x Triticosecale)* Wheat (15kg ha^{-1}) *(Triticum aestivum)*	Burr medic (1.85kg ha^{-1}) *(Medicago polymorpha)* Barrel medic (1.25kg ha^{-1}) *(Medicago truncatula)* Field peas (15kg ha^{-1}) *(Pisum sativa)* Berseem clover (1.25kg ha^{-1}) *(Trifolium alexandrinum)* Crimson clover (1.25kg ha^{-1}) *(Trifolium incarnatum)* Subterranean clover (2.25kg ha^{-1}) *(Trifolium subterraneum)* Common vetch (3.75kg ha^{-1}) *(Vicia sativa)* Woolly vetch (3.75kg ha^{-1}) *(Vicia villosa)*	Forage oats (12.5kg ha^{-1}) *(Avena sativa)* Flax (6.5kg ha^{-1}) *(Linum usitatissimum)* Burr medic (1.85kg ha^{-1}) *(Medicago polymorpha)* Field peas (15kg ha^{-1}) *(Pisum sativa)* Forage radish (1.25kg ha^{-1}) *(Raphanus sativa)* White mustard (1.25kg ha^{-1}) *(Sinapis alba)* Triticale (7.5kg ha^{-1}) *(x Triticosecale)* Woolly vetch (3.75kg ha^{-1}) *(Vicia villosa)*

Resource availability and capture

To investigate resource use by different cover crop mixes, we measured soil gravimetric water content, total mineral nitrogen, and percent of the ground covered by cover crops and by weeds (canopy cover), in each plot at three points throughout the season: approximately 50, 85 and 110 DAE. At each time point, four soil cores of a 4 cm diameter and 10 cm depth were taken from each plot and combined to form a representative soil sample. These soil samples were weighed wet, then dried at 60˚C for at least 72 hours, then weighed again to obtain the gravimetric water content. These samples were then tested for ammonium and nitrate content following indophenol-blue test (Keeney and Nelson 1982) and the salicylic acid method (Cataldo et al 1975), respectively. These two values were added together to obtain a value for total mineral nitrogen.

Canopy cover was visually estimated according to the Domin scale in three 1 m^2 quadrats in each plot, that were in fixed positions throughout the season to ensure biomass was not cut from these areas. Quadrats were located at 5m intervals along each plot, 0.5 m in from the edge (to avoid edge effects) on alternating sides of the plot; this meant quadrats were not disturbed during soil sampling down the centreline of the plots. Domin cover estimates were converted to the midpoint of each cover score (Lepš and Hadincová 1992), then these midpoints from the three quadrats were averaged to one representative value for each plot. Estimates were made by the same person to avoid observer bias.

In 2016, soil samples taken on the date of sowing (one representative sample per plot) were also tested for extractable phosphorus and sulphur, exchangeable calcium, magnesium and potassium, copper, zinc, manganese and boron content, according to methods set out by the Non-Affiliated Soil Analysis Work Committee (1990). These measurements were used to calculate differences in the soil nutrient content between the beginning and end of the season, to explore whether any treatments used more or less of each mineral, and thus to infer whether they may have played a role in competition between weeds and cover crops.

Subsequent cash crop year

Just prior to cash crop planting (late April) and at approximately 80 DAE, ground cover by cover crop and weed residue from the previous year was visually estimated in each plot (using the average of Domin estimates of two 1 m^2 randomly located quadrats). Also during the April pre-planting assessment, four soil cores 4 cm in diameter and 10 cm deep were collected at the April pre-planting assessment and combined to form a representative sample, then tested for total mineral nitrogen (as in Section 2.3.2).

In November, wheat grain from each plot at Langgewens was harvested using a plot combine harvester, with only a central 1m strip in each plot harvested to avoid edge effects. The grain was weighed to obtain a yield value in kg ha^{-1}. Final oat biomass samples were cut at Tygerhoek from three 0.25 m^2 quadrats located randomly along the centre line of each plot; these were combined to form a single representative sample for each plot. Oat biomass was separated from weed biomass, dried at 60˚C for 72 hours, and weighed.

Data analysis

Prior to analyses, all explanatory and response variables were standardised within each block, by subtracting the mean value of the replicate from the value for each plot, then dividing by the standard deviation. This removed variation in absolute values and variability due to differences between sites and years, to allow the identification of whether there was a consistent treatment effect across all sites and years. This procedure avoided the need for mixed modelling techniques in the analyses, as site and year as sources of random variation were accounted for by the standardisation.

To detect differences between mid and end-season weed and cover crop biomass, species diversity and functional diversity, we used analysis of variance (ANOVA) and post-hoc pairwise comparisons based on Tukey’s Honestly Significant Difference (HSD). If these were found to differ significantly ($P<0.05$) between mixes, linear regression models were used to explore whether these characteristics were linked to differences in soil nitrogen content, moisture content, and cover crop canopy cover at points throughout the season, or with differences in soil mineral levels between the start and end of the season. Adjusted R^2 values for all models are provided in the results as an indication of how well variation in the data is described by each model. All models were checked to ensure they fulfilled assumptions of normality and equal variance by assessing trends in the residuals, and also were checked for influential outliers; any issues are reported in the results. In cases where explanatory variables were collinear, separate models were created for each collinear variable, and the best model was chosen based on having a lower Akaike Information Criterion (AIC).

Linear regression models were also used to investigate: (a) whether weed biomass responded to resource levels; (b) whether the amount of each functional type of weed varied proportionally in response to the amount of different cover crop functional types in each mix; and (c) whether weed diversity was linked to cover crop diversity and/or biomass. To investigate cash crop yields in the subsequent years, ANOVA and Tukey's HSD were employed to test for differences between mixes, and regression models used to explore relationships between cover crop biomass and weed biomass in the cover crop year, residue cover at the start of the cash crop year, mid-season weed cover during the cash crop year, and cash crop yield. All analyses were undertaken in the software R, version 3.4.3 (R Core Team, 2017).

5.4 Results

Weed suppression by different mixes

Significantly lower final weed biomass was observed in the cereal and diverse mixes compared with most legume mixes (ANOVA $F = 19.46$, $P < 0.001$) (Figure 5.3). Of the legume mixes, 1L performed better than the others, and was the only legume mix to have significantly lower weed biomass than the bare-ground control.

Diversity, composition and productivity of different mixes

The species diversity (Shannon index) of the cover crop mixes was roughly as intended: the controls had zero diversity, the four-species mixes had an intermediate diversity, and the high species mixes had a higher diversity (Figure 5.4a; ANOVA F = 82.38, P < 0.001). However, the H-L mix did not have a significantly higher diversity than the 4-species mixes, as many of the legume species did not establish well, whilst the 4C mix had significantly higher diversity than both other four-species mixes, and the H-L mix. The Shannon index of functional diversity confirms that the 4D mix and HD mix were the only two mixes containing functional diversity, and furthermore that the HD mix had a higher functional diversity than the 4D mix (Figure 5.4b; ANOVA F = 106.4, P < 0.001). Biomass production differed substantially between mixes, with the cereal and diverse mixes producing significantly more cover crop biomass than the legume mixes (Figure 5.4c; ANOVA F = 34.53, P < 0.001). The 4L mix was not significantly different from the zero cover crop biomass produced by the bare-ground control.

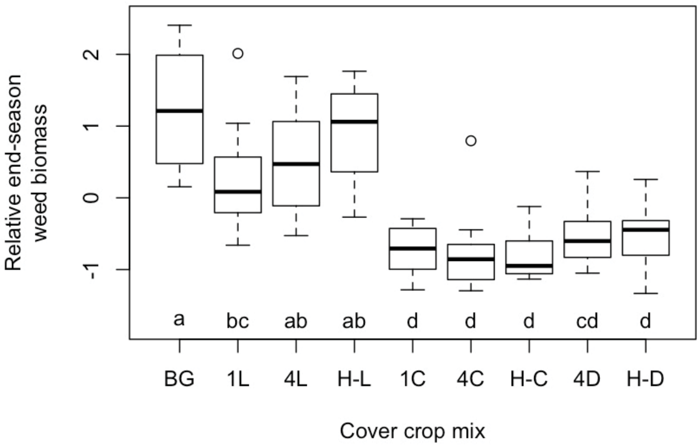

Figure 5.3: Relative final weed biomass in each of the cover crop mixes. Letters at the base of the plot indicate pairwise differences: mixes that are significantly different from one another do not share a letter.

Composition of the mixes varied as intended, with legume (L) mixes containing only legumes and cereal (C) mixes containing only cereals. The diverse mixes contained a mixture of cereals, legumes and brassicas, but their cereal components tended to be over-represented: 4D contained a mean cereal proportion of 0.69 (standard error, S.E. = 0.05), a mean legume proportion of 0.17 (S.E. = 0.06), and a mean brassica proportion of 0.13 (S.E. = 0.04). Similarly, the HD mix contained on average 0.61 cereals (S.E. = 0.04), 0.28 legumes (S.E. = 0.04), 0.1 brassicas (S.E. = 0.02), and 0.008 others (S.E. = 0.004); chicory or flax).

Mix characteristics and weed suppression

Of the cover crop characteristics of species diversity, functional diversity, composition and biomass production, only biomass production was associated with a reduction in weed biomass (Table 5.2, Figure 5.5). Increasing cover crop functional diversity was found to be associated with a small increase in mid-season weed biomass but this effect disappeared later in the season. The cover crop composition variables of cereal biomass and legume biomass were collinear with one another and also with total biomass, and could therefore not be included in the same model, so were tested in separate models. Results for the total biomass models only are displayed (Table 5.2), as cereal biomass consistently had a similar effect to total biomass (and legume biomass the opposite effect), but the AIC values for the models including either cereal or legume biomass were higher and the adjusted R^2 values lower, indicating poorer model fit. It was therefore concluded that cover crop composition determined how much biomass each cover crop produced, but did not directly affect weed biomass.

Mix characteristics and resource capture

Increased cover crop biomass was associated with increased canopy cover, at all points in the season and also with lower mineral nitrogen at 50 DAE (Table 5.3, Figure 5.6). This suggests that more productive mixes captured more light throughout the season and more nitrogen early

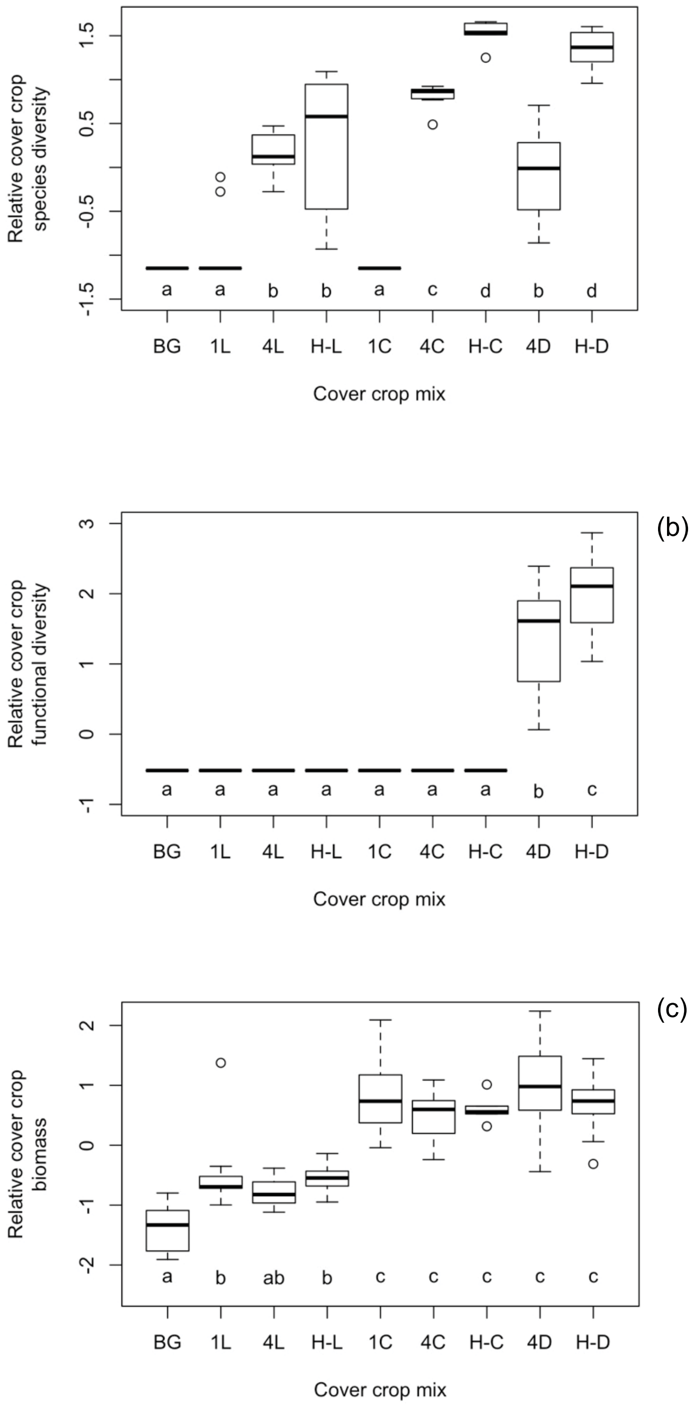

Figure 5.4: Relative Shannon species diversity (a), Shannon functional diversity (b) and biomass (c) in different cover crop mixes at the end of the season. Letters at the base of the plots indicate pairwise differences: mixes that are significantly different from one another do not share a letter.

Table 5.2: Results of the regression models between cover crop mix characteristics and weed biomass. 'Cover crop biomass' refers to mid-season biomass for the first two models (mid-season weed biomass and weed biomass increase) and end-season for the third model (end season weed biomass). The relationships between cover crop biomass and weed biomass are illustrated in Figure 5.5.

	Mid-season weed biomass		Weed biomass increase (mid to end-season)		End-season weed biomass	
	Estimate	*P-value*	*Estimate*	*P-value*	*Estimate*	*P-value*
Cover crop biomass	**-0.55**	**<0.001**	**-0.52**	**<0.001**	**-0.67**	**<0.001**
Cover crop species diversity	-0.01	0.938	-0.03	0.08	-0.14	0.075
Cover crop functional diversity	**0.22**	**0.03**	0.05	0.632	0.06	0.431
Adjusted R^2	*0.23*		*0.25*		*0.46*	

Table 5.3: Results of the regression models between cover crop biomass and resource capture. For the models at 50 DAE and 85 DAE, the explanatory variable is mid-season biomass, and for the models at 100 DAE the explanatory variable is end-season biomass.

	Nitrogen at 50 DAE		Nitrogen at 85 DAE		Nitrogen at 110 DAE	
	Estimate	*P-value*	*Estimate*	*P-value*	*Estimate*	*P-value*
Cover crop biomass	**-0.32**	**<0.001**	0.12	0.283	0.03	0.763
Adjusted R^2	*0.1*		*<0.01*		*<0.01*	
	Moisture at 50 DAE		Moisture at 85 DAE		Moisture at 110 DAE	
	Estimate	*P-value*	*Estimate*	*P-value*	*Estimate*	*P-value*
Cover crop biomass	-0.18	0.064	0.04	0.704	0.07	0.516
Adjusted R^2	*0.02*		*<0.01*		*<0.01*	
	Cover crop groundcover at 50 DAE		Cover crop groundcover at 85 DAE		Cover crop groundcover at 110 DAE	
	Estimate	*P-value*	*Estimate*	*P-value*	*Estimate*	*P-value*
Cover crop biomass	**0.79**	**<0.001**	**0.83**	**<0.001**	**0.67**	**<0.001**
Adjusted R^2	*0.62*		*0.69*		*0.44*	

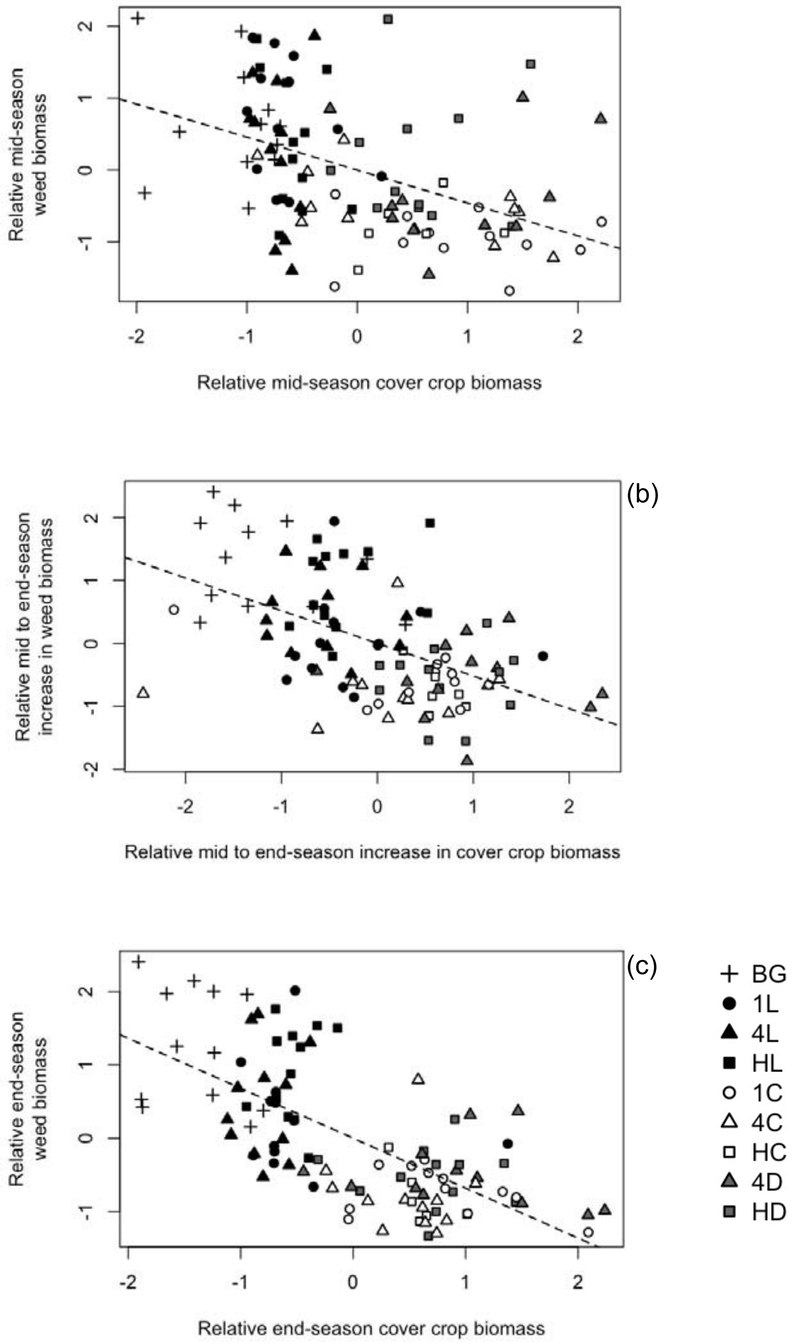

Figure 5.5: Plots of the relationships between cover crop and weed biomass throughout the season (Table 5.2): mid-season (a), increase between the middle and end of the season (b), and end-season (c). The dashed line indicates the linear regression line between the two variables.

in the season, although nitrogen uptake later in the season may have been obscured by the release of nitrogen from the mineralisation of crop residue and soil organic matter, when soils were sufficiently moist for this process to occur. None of the other soil minerals measured were observed to have any greater decreases in response to cover crop biomass (results not shown), indicating that the capacity of cover crops to suppress weeds was not related to the capture of any of these minerals.

Weed biomass and resource availability

Weed biomass increased in response to early-season nitrogen availability and to light availability throughout the season, although this occurred more strongly later in the season (Table 5.4, Figure 5.7). When nitrogen at 50 DAE and cover crop canopy cover at 85 DAE (the two resources most strongly associated with weed biomass; Table 5.4) are combined in a predictive model for end-of-season weed biomass, both are significant and the adjusted R^2 of this model is 0.51, indicating that approximately half of the variation in weed biomass between treatments can be explained by these two variables. In this model, the regression estimate for nitrogen at 50 DAE was 0.38 with $P < 0.001$, and the regression estimate for canopy cover was -0.51 with $P < 0.001$.

Limiting similarity and weed diversity

Thirty-six weed species were recorded in this study (Table 5.5). The weed community was overwhelmingly dominated by *Lolium* spp., which contributed 67% of total weed biomass in this study, across both farms and years. Proportions of different weed functional types did not vary significantly ($P>0.05$) in response to variation in the proportion of their corresponding cover crop functional types (results not shown), indicating that limiting similarity in terms of spatial resource capture traits did not occur. There was also no evidence to suggest that cover crop diversity increased weed diversity. However, if weed species diversity was standardised for weed biomass (by dividing the Shannon index of a plot by the biomass of that plot), then weed diversity increased as cover crop biomass increased (Figure 5.8). No such trend was observed for weed functional diversity.

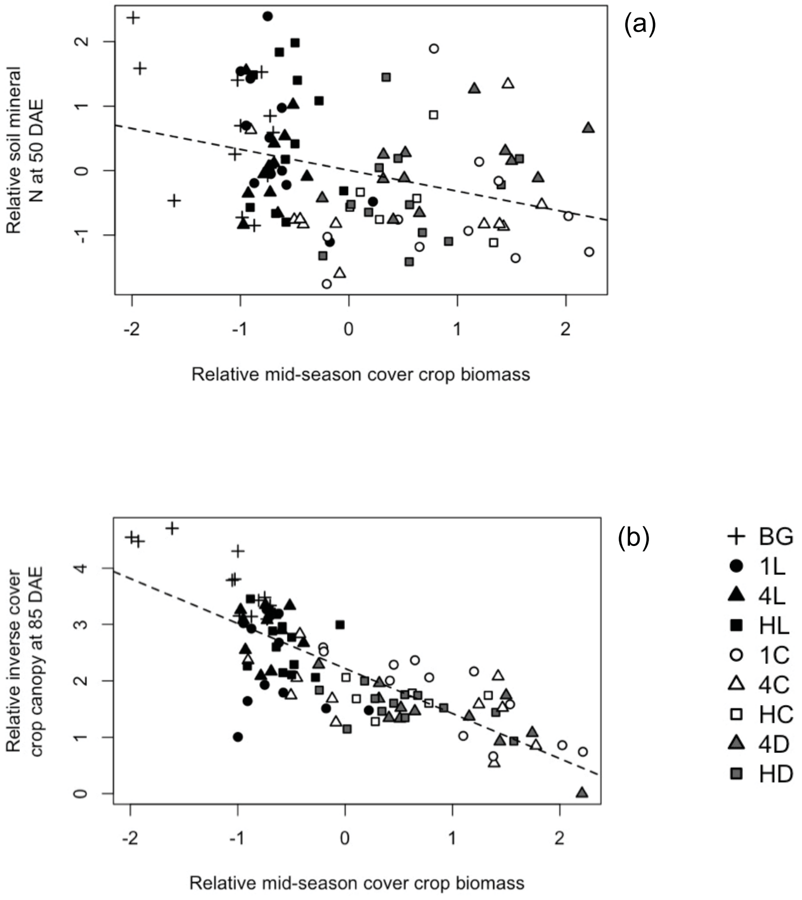

Figure 5.6: Illustrations of significant relationships between cover crop biomass and resource capture: (a) mid-season biomass and nitrogen at 50 DAE, (b) mid-season biomass and inverse canopy cover at 85 DAE. Canopy cover is displayed as the inverse so that the X axis represents increasing resource availability to weeds. Relationships for canopy cover at 50 DAE and 110 DAE (Table 5.3) were very similar to (b), but the adjusted R^2 was highest at 85 DAE indicating the strongest relationship between biomass and groundcover at this point in the season. Different mixes are identified by colour, and the grey line indicates the linear regression line between the two variables.

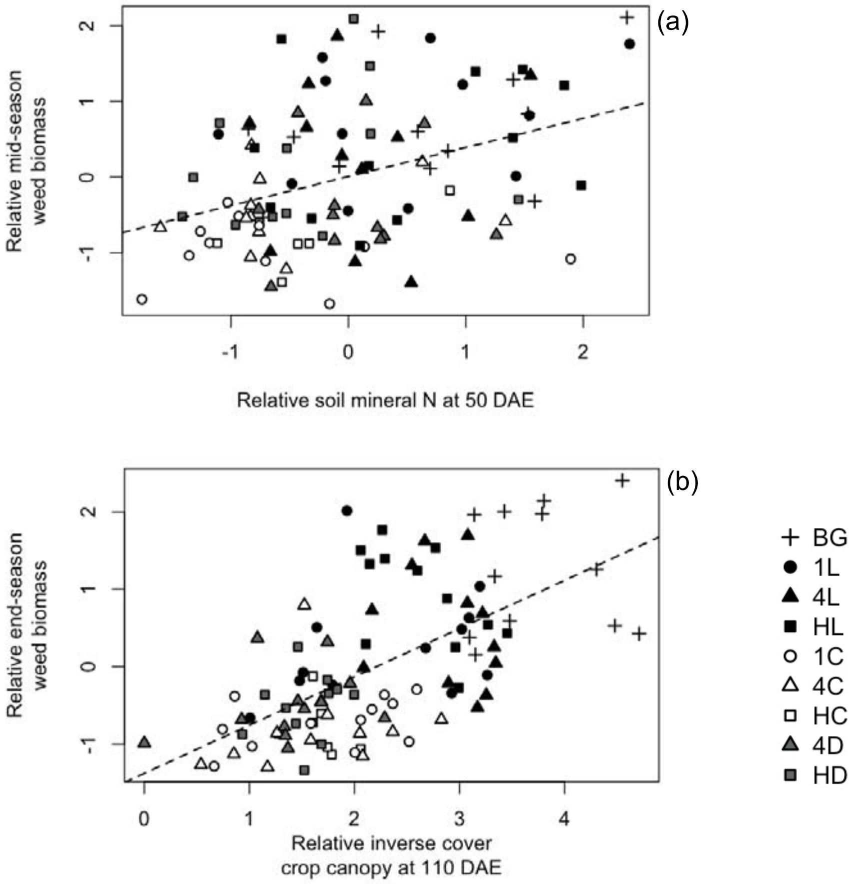

Figure 5.7: Significant relationships between weed biomass and soil nitrogen at 50 DAE (a), and cover crop groundcover at 110 DAE (b).

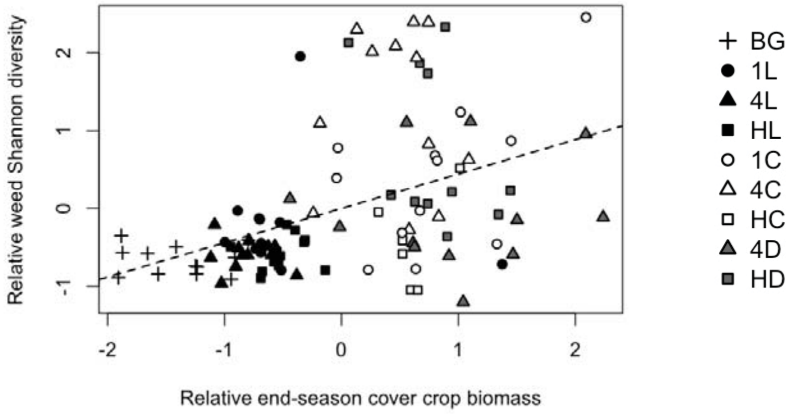

Figure 5.8: The relationship between relative weed species diversity and relative cover crop biomass. The grey line represents the regression equation between the two variables: the effect estimate for cover crop biomass on weed diversity is 0.44, with P <0.001.

Table 5.4: Results of univariate regression models between resource availability at different points in the season and weed biomass.

Univariate linear regression model for weed biomass	Estimate	P-value	Adjusted R^2
Nitrogen at 50 DAE	**0.38**	**<0.001**	**0.14**
Nitrogen at 85 DAE	0.07	0.474	<0.01
Nitrogen at 110 DAE	0.09	0.371	<0.01
Moisture at 50 DAE	0.01	0.887	<0.01
Moisture at 85 DAE	-0.05	0.592	<0.01
Moisture at 110 DAE	0.12	0.071	0.02
Cover crop groundcover at 50 DAE	**-0.29**	**0.004**	**0.07**
Cover crop groundcover at 85 DAE	**-0.58**	**0.001**	**0.33**
Cover crop groundcover at 110 DAE	**-0.59**	**<0.001**	**0.34**

Cover crop effects on cash crop yield in the following year

There were no significant relationships between cover crop mix and soil mineral nitrogen or cover crop residue at the start of the cash crop year, and neither of these parameters were associated with cash crop yield (Table 5.6). Mid-season weed cover in the cash crop yield was significantly associated with yield, although the relationship was weak (Table 5.6, Figure 5.9a). Whilst cover crop mix did not explain mid-season weed cover nor cash crop yield (results not shown), weed biomass in each plot in the cover crop year was associated with weed cover in the cash crop year (Figure 5.9b; regression estimate = 0.42, P = 0.003, Adjusted R^2 = 0.15) and was also weakly associated with cash crop yield (regression estimate = -0.27, P = 0.064, Adjusted R^2 = 0.05). Given that weed biomass decreased as cover crop biomass increased (Figure 5.3), this indicates that cover crops can affect cash crop yields via weed suppression in the cover crop year leading to reduced weed pressure in the subsequent cash crop year.

Table 5.5: The weed species found, their functional type (see end of Section 2.2), and their average proportional biomass across all plots in the trial. Functional types are G = grass, SH = short, prostrate or rosette-forming herb, TH = tall upright herb. Some species are volunteers from the main crops grown on the research farms (wheat, canola, forage legumes). Both *Lolium* and *Conyza* species hybridise within their genus and were not identified to species level.

Species	**Functional type**	**Average proportional biomass**
Anagallis arvensis	SH	<0.01
Avena fatua	G	0.03
Bromus catharticus	G	<0.01
Bromus diandrus	G	0.04
Brassica napus	TH	0.03
Chenopodium album	TH	<0.01
Conyza spp.	TH	<0.01
Erodium moschatum	SH	<0.01
Euphorbia inaequilatera	SH	<0.01
Fumaria officinalis	SH	<0.01
Helminotheca echioides	SH	<0.01
Hypochaeris radicata	SH	<0.01
Lactuca serriola	SH	<0.01
Lepidium africanum	TH	<0.01
Lolium spp.	G	0.67
Malva parviflora	TH	<0.01
Medicago lupulina	SH	0.01
Medicago polymorpha	SH	0.01
Medicago truncatula	SH	<0.01
Plantago lanceolata	SH	<0.01
Polygonum aviculare	SH	<0.01
Pseudognaphalium luteoalbum	TH	<0.01
Raphanus raphanistrum	TH	<0.01
Rumex acetosella	SH	<0.01
Sonchus oleraceus	SH	0.02
Taraxacum officinalis	SH	<0.01
Triticum aestivum	G	0.12
Trifolium repens	SH	<0.01
Vicia sativa	SH	<0.01
Unknown species (8 morphotypes)		<0.01

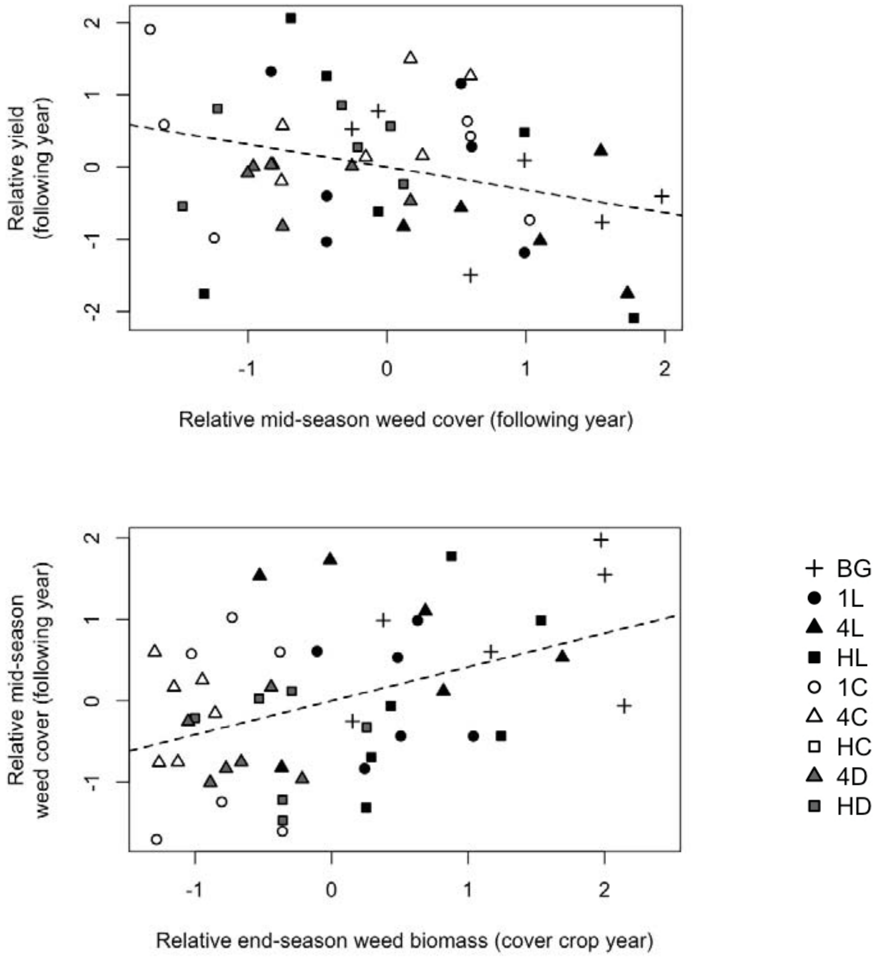

Figure 5.9: Cash crop yield declines as mid-season weed cover in the cash crop year increases (a), and weed biomass in the cover crop year affects mid-season weed cover in the cash crop year (b).

Table 5.6: Results of the regression models of the relationships between weed cover, soil nitrogen, residue cover and wheat yield the year following the cover crop treatments.

Univariate model for yield	Estimate	P-value	Adjusted R2
Mid-season weed cover	**-0.32**	**0.029**	**0.08**
Start-of-season soil nitrogen	0.02	0.918	-0.02
Start-of-season residue cover	0.04	0.766	-0.02

5.5 Discussion

Cover crop diversity, resource capture, weed suppression and weed diversity

This study confirms that cover crops can be effective in suppressing weed biomass through reducing the availability of resources to weeds. However, neither species diversity nor functional diversity (in terms of the spatial resource capture traits explored in this study) increased the efficacy of cover crops in this regard (hypotheses A and B). There was also no evidence to suggest that cover crops with a particular growth form and root architecture suppressed weeds with comparable traits, and thus no evidence for limiting similarity (hypothesis C). Our results indicate that the cover crop mixes that produced the most biomass were able to capture resources most effectively and were most able to suppress all types of weeds. The most productive mixes were either composed entirely of cereals, or were diverse mixes dominated by cereals and brassicas.

These findings agree with previous trials of cover crops that found that cover crop species able to produce a large quantity of biomass quickly are most capable of suppressing weeds (Palmer and Maurer 1997, Brennan and Smith 2005, Storkey et al 2011, Brust et al 2014, Smith et al 2014, Smith et al 2015), and that diversity does not necessarily result in increased function in this regard (Finney et al 2016). Additionally, recent studies on biotic resistance to alien plant invasions suggest that fitness differences between resident species and invaders determine resistance to a greater extent than resident diversity, or the functional similarity of dominant resident species to the invader (Byun et al 2013, Funk and Wolf 2016). In the context and conditions of this study, cereal and brassica species were most capable of capturing resources and producing biomass rapidly, and thus had the greatest fitness advantage against weeds.

However, some studies of cover crop mixes have found an increased ability of diverse mixes to suppress weeds (Linares et al 2008, Döring et al 2012a), and several studies on plant invasions have found some evidence that functional group diversity increases resistance to invasion at scales comparable with this study, albeit less so than the fitness of dominant resident species (Richardson and Pyšek 2006, Byun et al 2013). It is possible that this effect of diversity would be seen in cover crops if all species included in a diverse mix are adequately competitive. This idea is supported by the findings of Wortmann et al (2012) and Smith et al (2014) that cover crop mixes typically have a Land Equivalent Ratio > 1, producing more biomass than can be accounted for by the productivity of each species grown in monoculture. Therefore, creating mixes containing only highly productive species may result in more effective weed suppression than a monoculture, whilst also increasing opportunities for multifunctionality through diversity. In this study both functionally diverse mixes contained at least two legume species, which produced substantially less biomass than the cereal and brassica species, and may therefore have negated any effect of diversity.

Previous trials on diverse cover crops and forage crops suggest that functional diversity in terms of phenology, rather than the spatial resource capture traits tested in this study, may be more important to weed suppression (Porqueddu et al 2008, Döring et al 2012b, Finn et al 2013). In this regard, it is the capacity of different species to capture resources and produce biomass at different points in the season (or in subsequent years in long-term leys) that results in greater overall weed suppression. This suggests that if limiting similarity does occur between crops and weeds, it may also be a largely phenological phenomenon, and that crops and weeds with high simultaneous resource demands may be most likely to compete with one another.

In addition to finding no evidence that cover crop diversity promotes weed suppression, we also found no evidence that it increases weed diversity (hypothesis D). However, when standardised by biomass, weed species diversity was higher where cover crop biomass was higher, a trend that may be due to abundance of the dominant *Lolium* spp. being suppressed to a greater extent by cover crop biomass than other weeds. This may be an example of phenological limiting similarity: both *Lolium* and the most productive cover crops (the cereals) are more productive earlier in the season and thus may compete more for resources with one another than with legumes or other weeds. Phenological data on the weeds in the trial location was not available, but this effect could be further explored.

Differences between cover crop types

The cereal species included in this study were found to suppress weeds more effectively than the legume species (the brassicas and ‘other’ species were included in too few treatments to draw conclusions on their overall competitiveness). A key mechanism that appeared to give cereal cover crops a fitness advantage over weeds was rapid nitrogen capture early in the season, followed by restricting light availability to weeds later in the season. However, the availability of those two resources could only explain approximately 50% of the variation in weed biomass between mixes, suggesting that competition for other resources, or allelopathy, may also have played a role. There is evidence that several of the cover crop species included in this trial are allelopathic (Jabran et al 2015, Rueda-Ayala et al 2015). Thus, it is plausible that cover crop biomass suppressed weeds through both allelopathy and competition for nitrogen and light. It is also possible that legumes increased weed biomass through a facilitative effect on weeds: although most nitrogen fixed by legumes becomes available in the following season as their residues decompose, some nitrogen can be transferred from legumes to other plants within the first growing season (Pirhofer-Walzl et al 2012). However, given the overall low biomass produced by legumes, it is expected that any facilitative effect would be small.

The faster resource uptake and greater weed suppression of cereals compared with legumes was linked to differences in biomass production. This may be explained by life-strategy differences between these two crop types, with cereals appearing to have a ‘faster’ life strategy (Reich 2014) than legumes, which may have been enhanced by breeding for yield and competitiveness. Typically, plant species with a faster growth rate invest fewer resources in resilience to stress and disturbance, and thus would be capable of using those resources to produce more biomass to further enhance resource uptake (Garnier and Navas 2012, Reich 2014). Legumes may be constrained in their growth relative to cereals due to the need to direct sugars to feed their rhizobial mutualists and by investment in mechanisms that allow them to recover from grazing, as many of the legume species included in this trial were forage species.

However, a study by Tribouillois et al (2015) on cover crop traits found no evidence to suggest that cereals inherently grow faster or capture more nitrogen than legume crops in conditions of non-limiting resources. This suggests that the conditions in this study may have disadvantaged legumes compared with cereals, brassicas and weeds. Sowing depth may have been a constraint: in this trial the disc planter placed the seeds at approximately 15 mm below the soil surface, which is considered shallow for cereals but deep for legumes, apart from the larger-seeded legumes (vetch and pea), which typically performed better. The climatic conditions during the trial may also have played a role, with the first rainfall arriving later into winter in both years than is usual for the region. Legume varieties used in the region may not have been bred to tolerate such low soil temperatures when sufficient moisture becomes available for germination and establishment. Thus, we would not conclude from this study that cereal cover crops would always outperform legumes in competition against weeds.

Weeds and resource availability

That we were able to predict nearly half of weed variation within a replicate based on nitrogen and light availability confirms the need to consider resource uptake capacity when choosing which species to include in a mix. In this regard, the main trait of interest in cover crops is their capacity to produce biomass, as shown in this study and confirmed by other trials of weed suppression by cover crops (Palmer and Maurer 1997, Brennan and Smith 2005, Storkey et al 2011, Brust et al 2014, Smith et al 2014, Finney et al 2016). The timing of that productivity may also be important (Döring et al 2012b, Finn et al 2013), but was not investigated in this trial.

The weed response to nitrogen and light observed in this study also has implications for other farm management practices beyond cover cropping, suggesting that resource availability to weeds should be considered and reduced wherever possible. Recent techniques in precision agriculture may offer improvements. The finding is also relevant to breeding of both cover crops and cash crops: rapid early growth and resource capture may be the best defence against weed competition throughout the season.

Cover crops, weeds, and cash crop yield in the following year

This study suggested a weak link between cover crop performance in weed suppression and subsequent cash crop yield, mediated by reduced weed cover following productive cover crops (hypothesis E). That a stronger effect on yield was not observed may have been partially related to several of the most weed-suppressive cover crop species (the cereals) returning as volunteer weeds in the subsequent cash crop, thus countering their contribution to weed suppression. Cover crop mixes present a challenge for non-chemical termination, as the roller-crimper technique is only effective in a short time window when cover crop plants are mature enough to be vulnerable, but have not yet set seed, and this time window may not overlap between all species in a mix. This effect may have allowed the cereals in this trial to either produce viable seed before termination, or recover to set seed afterwards.

There are also other characteristics of cover crops that contribute to subsequent cash crop yields aside from weed suppression (Snapp et al 2005, Blanco-Canqui et al 2015, Wittwer et al 2017). The addition of nitrogen to the soil by legumes is an important factor (Bedoussac et al 2015), and thus what the legume mixes lacked in weed suppressive capacity they may have made up for by providing nitrogen or reducing pathogen survival. Although soil nitrogen content at the start of the cash crop season was not associated with cash crop yield, further nitrogen may have been released to the cash crop from legume residues throughout the season.

Implications for design of cover crop mixes

The results of this study indicate that the recent enthusiasm for diverse cover crop mixes should be tempered with a focus on including sufficient quantities of species that are known to perform key functions effectively. In this regard, our results agree with those of Storkey et al (2015) who found that multifunctionality was best achieved by the inclusion of four species which each performed a specific function well, ideally with one of those species being a generalist capable of performing all desired functions well. Finney et al (2016) suggest that biomass-driven functions of cover crops, such as weed suppression, are best achieved by selecting the most productive species rather than basing mixes on functional complementarity.

A diverse cover crop mix can offer many advantages to farmers in terms of multifunctionality (Malézieux et al 2009, Isbell et al 2017), and so rather than avoiding diversity for the sake of weed suppression, we recommend that multi-species mixes are composed with a strong emphasis on the competitive ability of each species included in the mix. It is important to ensure that cover crop mixes that are recommended or provided to farmers do not lead to increases in weed pressure and thus provide a disincentive for farmers to continue cover cropping, given the advances in agricultural sustainability offered even by monocultural cover crops (Anderson 2015, Wittwer et al 17). Future research on improving cover crop mixes for weed suppression could therefore focus on the identification of highly productive (and therefore weed-suppressive) cover crop species and cultivars from a variety of plant families that could be combined in multispecies mixes that are appropriate to the farming systems in question. For example, our finding that cereals and perhaps brassicas are the most effective weed-suppressing cover crops in the Swartland and southern Cape of South Africa is not the most practical recommendation for the region’s farmers, whose main cash crops are wheat, barley and canola. Closely related cover crop species run the risk of bridging pests and pathogens between cash crop years (Krupinksy et al 2002), and avoiding legumes leaves farmers burdened with the environmental and economic costs of synthetic nitrogen fertiliser (Bedoussac et al 2015). Research on identifying and developing new cover crops is ongoing in central Europe (eg. Brust et al 2014, Thorup-Kristensen and Rasmussen 2015), but similar efforts will be needed in other regions to develop cover crops that suit the different climates, soils and farming systems around the world.

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5.7 Author contributions

CM designed the study with contributions from KD, PS and JB. CM undertook the data collection and analysis with advice and assistance from PS, and CM drafted the article. All authors contributed to revising and improving the article.

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CHAPTER 6: DISCUSSION

6.1 Introduction

The overarching aim of this thesis was to explore options for the ecological intensification of weed management in South Africa's winter rainfall region, to improve agricultural sustainability in the face of the region's specific challenges and conditions. To achieve this, the thesis began with an up-to-date review of ecological processes that influence the abundance, composition and diversity of weeds in cropping systems, and used this review to identify possibilities for implementing these processes in agroecosystems (Chapter 2). This was followed by three practical studies and trials that explored or tested the most promising of these ideas for farms in South Africa's winter rainfall region. Each of the chapters in this thesis aimed both to test theories in weed ecology, and to make practical contributions to sustainable weed management in South Africa's winter rainfall region. In this discussion chapter, the main findings of the thesis are thus evaluated in terms of its implications for a) weed ecology theory, b) sustainable weed management in South Africa's winter rainfall region, and c) sustainable weed management and research in general.

6.2 Implications for weed ecological theory

Ecology is the science that underpins the sustainability of weed management: it not only describes the dynamics of weed populations and communities, but also describes how both weeds and weed management interact with other elements of the agroecosystem and the wider environment. The ecological intensification of weed management involves identifying and harnessing those ecosystem processes that limit the negative impacts of weeds on productivity, whilst conserving weed (or 'wild plant') diversity and their positive functions in agroecosystems. This can reduce anthropogenic inputs (Bommarco et al 2015), and thereby enable agriculture to reduce pressure on Earth's life-supporting ecosystems whilst continuing to meet human needs (Rockström et al 2009, Raworth 2012, Steffan et al 2015). Given that ecological intensification practices are based on our understanding of ecology, testing these practices allows for a dialogue with ecological theory: which practices do we expect to be effective in weed management and why? When we implement these, do weeds respond to management practices as we would expect? If not, why not? Is further research required to clarify the results observed? This section explores how the previous chapters in this thesis address these questions, both separately and when taken together.

Chapter 2 – ecological strategies for increasing agroecosystem resilience to weeds:

As a conceptual framework for integrating ecological processes into farming systems for weed management, the review (Chapter 2) emphasised the importance of focusing on 'agroecosystem resilience to weeds' rather than on managing the weeds themselves. If farming systems can be designed not to present opportunities for weeds to proliferate, then specific efforts required to suppress weeds can be reduced, and some level of weed cover can be encouraged for its contributions to biodiversity support and ecosystem services (Blaix et al 2018). A key characteristic of a system resilient in this way would be its capacity to self-regulate, and thus key ecological processes to seek to implement would be those that regulate weed quantity and weed quality. Chapter 2 identified several such processes, including appropriate management of the strength, diversity and direction of ecological filters and selection pressures imposed on weeds, and management of the quantity and diversity of resources available to weeds. The chapter concluded by exploring practices that can initiate or facilitate these processes in agroecosystems (Table 2.1).

Chapter 2 thus offered a substantial contribution to knowledge in weed science by drawing together many disparate but relevant ecological processes to form a foundation to explain the success of existing weed control practices and identify potential for new practices. Other recent reviews of weed science for weed management have tended to focus on the tools available for weed management (Shaner and Beckie 2013, Bajwa et al 2015, Westwood et al 2018), rather than focusing on the ecological processes that underlie why or why not these tools are more or less successful in different situations. This review is therefore more valuable to suggest new possibilities for sustainable weed management, and to improve our capacity to choose the right tools for the right situation and fit them to the overall farming system. Each of the subsequent practical chapters in this thesis explored turning some of these possibilities into practices for South Africa’s winter rainfall region. Their implications for the ecological theories described in Chapter 2 are summarised in Table 6.1, and explored in more detail below.

Chapter 3 – directional selection and filter intensity to manage weed community composition:

The first practical chapter used the functional trait response-effect framework (Lavorel and Garnier 2002) to explore whether weed communities differ in their relative costs and benefits to the surrounding agroecosystem, and whether different management practices could be used to select for weed communities that provide more environmental benefits whilst imposing lower competition against crops. Trends observed in this study (undertaken on vineyards) provided evidence for the theoretical trait dimensionality of plants outlined in Figure 2.3, that the reduced disturbance imposed by mowing and organic practices compared with tillage and herbicides selected for ‘slower’ and less ruderal traits in terms of shorter weeds with fewer, larger seeds. Sites with a high resource availability also had weeds with a higher SLA, representing a ‘faster’ life history strategy (Figure 3.2).

As explored in the discussion section of Chapter 3, these results suggest that conventional agricultural practices, including reliance on synthetic fertilisers and heavy disturbance via herbicides and/or tillage to suppress weeds, tend to select for more problematic weeds. In contrast, alternative practices such as organic systems that minimise tillage do not increase resource availability and disturbance to such an extent, and thus selection pressure for problematic ‘fast’ species is reduced. These results agree with the findings of several other studies (e.g. Fried et al 2009, Storkey et al 2010, José-María et al 2011) who also found that weeds with traits such as small seed size and faster growth rates increase as conventional agriculture practices intensify.

Overall, the concepts of reducing management intensity to promote weed diversity, and using directional selection to promote beneficial weeds over problematic weeds, are relatively new in the field of weed science with few papers exploring this so far (but see Storkey 2006, Storkey and Westbury 2007, Mézière et al 2015). It seems a promising approach to balance the need to conserve weeds for biodiversity and ecosystem services with the need to minimise the negative impacts of weeds on crops. Further research is definitely required, as for example, 'fast' weeds may not necessarily be problematic in all situations: they may improve nutrient cycling and be easier to suppress by increasing herbivory, as species with a higher specific leaf area and high leaf nitrogen content tend to decompose more rapidly and be more palatable to herbivores (Wardle et al 2002, Kazakou et al 2016). In addition, 'slow' species may be more competitive in resource-limited environments (Reich 2014), such as dryland agriculture in low rainfall areas. Exploring some of these uncertainties could be combined with experiments to confirm that changes in management do cause changes in weed community composition, for example, a trial that explores the effect of ceasing herbicide use and initiating a mowing regime could be accompanied by measures of arthropod diversity and soil moisture and nitrogen fluxes under different weed communities. Such trials would allow further progress in fundamental weed ecology whilst also refining practice to increase the sustainability of farm management.

Chapter 4 - temporal filter diversity to suppress weed abundance and promote diversity:

Chapter 4 explored the role of temporal diversity in both crops and management practices in limiting weed abundance whilst promoting weed diversity, through varying ecological filters and selection pressure between years. Whilst this theme has been frequently explored in weed science, Chapter 4 identified two important points that so far seem to have been overlooked in weed science. Firstly, using different management practices with diverse selection pressures (herbicides and grazing) was found to be more important than using different practices with more similar selection pressures (different types of herbicides). Regardless of one's position on the environmental and health risks of herbicides, this study shows that it is more effective to alternate herbicides with non-chemical management rather than to simply increase the diversity of herbicide mode-of-action groups, which can still select for traits that confer general herbicide resistance or avoidance. This emphasises the need to seek non-chemical alternatives in weed management.

Secondly, diversity in management and conditions between years is more important than using a diversity of tactics (or ‘little hammers’; Liebmann and Gallandt 1997) within each year. This does not seem to have been previously explicitly articulated in the literature, although it is evident from the relative success of weed management trials that vary conditions between years (e.g. Davis et al 2012, Anderson 2015, Blackshaw et al 2015) compared with those that combine multiple weed management actions within a year (e.g. Chikowo et al 2009, Benaragama et al 2016). It could be useful to explicitly test this finding in a future long-term study, and also to investigate different management practices to those explored in Chapter 4; e.g. does alternating grazing and mowing have a sufficiently distinct effect to be useful in organic farms seeking to reduce tillage? If herbicides are used only once every three years in rotation with tillage or grazing, is their effect the same as when herbicides are used every year on increasingly tolerant or resistant weed communities? Using different management options in different years potentially gives farmers more flexibility (Bell et al 2014), and may be more cost-effective, than attempting to combine multiple management actions every year. Future research on different management combinations could allow farmers to optimise the use of the tools available to them, and further minimise those that have negative impacts on sustainability.

Chapter 5 – cover crop diversity for complementary resource capture and weed suppression:

Chapter 5 assessed the role of cover crop productivity, functional diversity and species diversity in resource capture and weed suppression. The experiment provided evidence that reducing resource availability can be effective for weed suppression, and that productive cover crops can be useful in this regard. However, diversity did not increase the capacity of a cover crop mix to capture resources and suppress weeds; it is instead more important that the mix is composed of species with traits that confer rapid resource uptake. In this regard, the results agree with those of other researchers who have noted that crop species with traits reflecting a ‘faster’ life strategy (Reich 2014, Andrew et al 2015) are typically most competitive with weeds in agroecosystems. Similar trends are evident in plant invasions of natural ecosystems following disturbance: species that are productive and capable of rapid resource capture at the same time that the invader requires those resources are most able to suppress invasions (Byun et al 2015).

The strong relationship between cover crop productivity and weed suppression also supports Storkey et al’s (2015) and Finney et al’s (2016) conclusion that different functional types of cover crop are best utilised for their ability to perform different functions, to achieve mix multifunctionality. Despite the fact that mixes can produce a land equivalency ratio greater than 1 (Wortman et al 2012), it does not seem that we can use this niche complementarity to increase weed suppression, as might be expected from the theory outlined in Díaz and Cabido (2001) and Funk et al (2008). This may result from a lack of availability of crop species that are sufficiently competitive for niche complementarity to outweigh the benefit of using the single most productive species. However, it is also possible that niche complementarity has a stronger effect in time rather than space, as other studies have identified that diverse mixes including species that are more productive in different seasons are more able to suppress weeds in longer term leys (Finn et al 2013).

	Diverse selection pressure	Directional selection pressure	Alternate selection pressure	Appropriate disturbance	Resource availability	Resource diversity	Exploit weed benefits
Chapter 3: Management to minimise competition/ biodiversity trade-off		Specific management techniques can be used to select for traits that minimise competition (e.g. mowing to reduce height in vineyards, reduced disturbance to reduce selection for 'fast' life history strategies)		Management types that impose weaker filters permit greater weed diversity	Higher resource availability associated with 'faster' life history trait (SLA)		More diverse weed communities expected to offer higher value to biodiversity
Chapter 4: Integrated crop-livestock rotations	Diverse selection pressure (crop diversity and management diversity) reduces weed quantity and increases diversity		Integrating management techniques with different selection pressure (herbicides and grazing) is more effective than those with similar pressure (multiple herbicides)	Stronger disturbance (more herbicide applied) did not reduce weed abundance	Rotations with less synthetic fertiliser applied had fewer weeds	Rotations containing legumes and livestock in addition to small grain crops had more diverse weeds	*Lolium spp* and *P. aviculare* that are promoted by cash crops can be utilised by livestock
Chapter 5: Diverse cover crop mixes			Competitive cover crops can suppress weeds, and could thus be included as part of a diverse weed management strategy		Cover crops that reduced resource availability most effectively limited weed abundance; however, cover crop composition was more important than diversity to achieve this		

Table 6.1: A summary of contributions to the ecology of weed management made by each chapter of this thesis, with reference to the processes identified in Table 2.1.

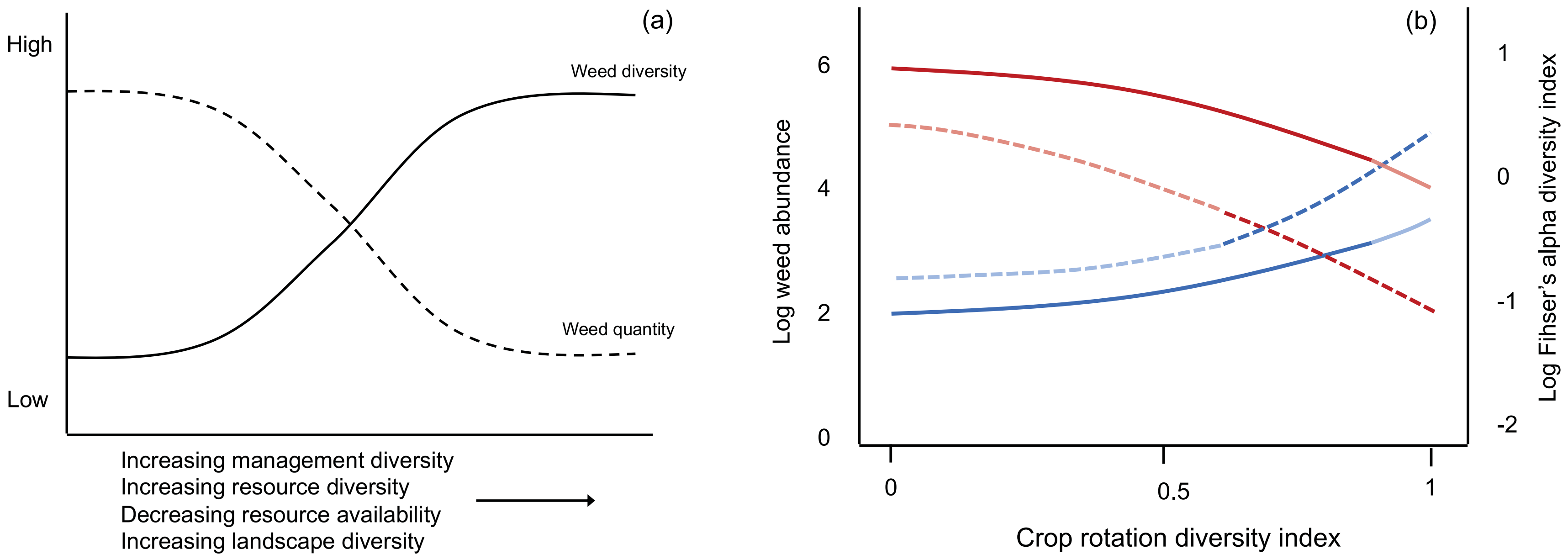

Figure 6.1: (a) A reproduction of Figure 2.4 - predicted trends in weed abundance and diversity based on weed ecology theory. (b) Similar trends in weed abundance and diversity observed in Chapter 4 in the long-term response of weeds to integrated crop-livestock rotations, summarised from Figure 4.4. The red lines indicate weed abundance and the blue line diversity; the solid lines indicate rotation systems with no livestock, and dashed lines indicate systems with integrated livestock (and thus incorporate increased management diversity, increased resource diversity and decreased resource availability). Light coloured parts of the lines are extrapolations to diversity-livestock combinations that were not included in Chapter 4's long-term trial. In Chapter 3, a similar trend was found to occur for diversity when the strength of the management filter decreases from sprayed sites in conventional vineyards compared to mown sites in organic vineyards (Figure 3.3). Chapter 5 describes a similar trend for weed abundance as resource availability to weeds is reduced by competition from cover crops.

Summary of contributions to weed ecology

Table 6.1 summarises the ecological processes identified in Chapter 2 that have potential to increase resilience to weeds in farming systems, and the contributions provided by each practical chapter to furthering understanding of the functioning of those processes. Combined, the three practical studies indicate that increasing diversity and reducing filter strength and resource availability in farming systems contributes to limiting weed abundance whilst conserving weed diversity (Table 6.1, Figure 6.1). This finding was most explicit in the effects of crop and management diversity on weeds investigated in Chapter 4, but further supported by the links between mowing (a softer filter) and increased weed diversity in Chapter 3, and the relationship between resource availability and weed abundance observed in Chapter 5. Although each of these themes of filter diversity, filter strength and resource availability have been explored on by many other authors (e.g. Navas 2012, Gaba et al 2013, Smith 2015, Storkey and Neve 2018), this thesis presents the first synthesis of these into theoretical frameworks to explain weed abundance and diversity (Figures 2.4 and 6.1) and weed functional community composition by life history traits (Figure 2.3). These frameworks provide a useful basis for identifying which ecological properties and processes can be employed in farm management strategies to enhance agroecosystem resilience to weeds.

In addition, each chapter was able to test specific aspects of theory that remain unclear in the general literature and thus make novel contributions to weed science. The role of management diversity within the effect of crop rotation had not previously been clarified, and the role of functional diversity in the biotic resistance of annual cover crops to weeds had not previously been explored. This demonstrates that using ecological theory to design management techniques can advance our knowledge of weed ecology as well as identifying practical techniques that can be integrated into farming systems. The next section explores how this approach also contributes to developing more sustainable farming practices. More weed ecologists would thus be encouraged to test their theories as part of trials of farm management, whilst more weed managers should seek inspiration for new approaches in ecology. The approach can advance both fields simultaneously.

6.3 Practical implications for weed management in South Africa's winter rainfall region

Addressing the region's key challenges in weed management

Each of the practical chapters in this thesis was designed to explore or test a specific practice that had potential to improve the sustainability of weed management in South Africa's winter rainfall region. This section discusses what actions the results suggest can be taken to modify farming practices in the region, both from the perspective of meeting human needs as well as protecting the environment (i.e. moving toward Raworth's 'safe and just space', Figure 1.1). Key needs for weed management in the region were identified as (see Chapter 1):
a) avoiding intensive herbicide use or soil disturbance;
b) effectiveness against herbicide-resistant weeds, especially *Lolium* spp.;
c) achievable and economically feasible with available crop species and tools;
d) contributing to restoring natural biodiversity and ecosystem functioning.

The findings of the practical chapters each make useful contributions to addressing these challenges, which are summarised in Table 6.2, and discussed below in turn. Finally, the findings of all chapters are drawn together to make recommendations for changes to farming systems, and identify remaining research gaps.

Alternatives to herbicides for no-till systems

Reliance on herbicides for weed management is unsustainable for multiple reasons: herbicides can cause environmental pollution (Relyea 2005, Annett et al 2014), damage human health (Mamane et al 2015, Myers et al 2016), impact soil microbial communities (Druille et al 2013), inhibit crops (Rose et al 2017), and promote the development of herbicide resistance, which limits the lifespan of herbicides' utility in weed management (Neve et al 2009, Mortensen et al 2012). The findings of this thesis, alongside other similar studies (see Garnier and Navas 2012), also suggest that the strength of the filter imposed on weeds by herbicides may select for weeds that are more competitive and harder to control (Chapters 3 and 4), particularly in annual cropping systems, due to their fast growth rates and high numbers of propagules. Thus, the ability of herbicides to concurrently meet the human needs of agriculture (food, fuel and fibre production) both now and in the future whilst avoiding ecosystem degradation is low.

The most effective way to solve the problems associated with herbicides would be to replace herbicides with alternate weed management strategies; however, that is much easier said than done. For instance, in regions such as South Africa's winter rainfall region where conservation agriculture practices make a substantial contribution to sustaining soil health, non-chemical options for weed management are limited. This thesis explored several alternatives to herbicides that could help to address this. It did so by building on techniques that were identified as promising in previous literature (e.g. Gaba et al 2013, Bajwa et al 2015, Liebmann et al 2016) and for which Chapter 2 identified a sound theoretical base to expect positive impacts on weed management.

Chapter 3 indicated that reducing herbicide use could promote the positive functions of weeds whilst reducing their negative functions. It was inspired by previous studies suggesting that 'optimal' weed communities composed of species that offer high value to biodiversity whilst imposing low competitive potential with crops could be achieved with the right management (Storkey 2006, Storkey and Westbury 2007, Mèziére et al 2015) and the results of Chapter 3 suggest this can best be achieved with a 'soft' management filter, such as mowing. Other studies also suggest that reducing herbicide use may be beneficial to weed management, particularly when the positive functions of weeds are considered. One key study summed up succinctly by its title is 'Herbicides do not improve yields but kill rare plants' (Gaba et al 2016), whilst Blaix et al's (2018) review highlights the ecosystem services that weeds can provide both to promote agricultural

Table 6.2: Summary of each chapter's contribution to addressing specific weed management challenges in South Africa's winter rainfall region.

	Alternatives to herbicides for no-till systems	**Specific measures to reduce dominance of *Lolium* spp.**	**Using weeds to promote biodiversity in the Cape Floristic Region**	**Achievable and feasible with available crop species and tools**
Chapter 2: Ecological strategies for resilience to weeds (review)	Identified a range of non-herbicide and non-tillage farm practices that could improve weed management.	Identified that increasing management diversity and reducing resource availability are key to reducing the dominance of problematic species.	Identified practices that can promote weed diversity, and can thus increase the role of weeds in supporting biodiversity at higher trophic levels, conserving weed diversity can contribute to conserving native plants that occur as weeds.	Several of the identified practices from this chapter are amenable to South Africa's winter rainfall region, as explored in Chapters 3 – 5.
Chapter 3: Management to minimise competition/ biodiversity trade-off	Reducing herbicide use in vineyards in favour of mowing may reduce weed competition with crops and promote biodiversity.	*Lolium* was less dominant in organic mown or tilled vineyards compared to vineyards managed with herbicides.	Vineyards managed primarily with mowing had a higher diversity of weeds, and a higher proportion of native plant species as weeds.	Mowing is already used as the primary management tool by most organic vineyard farmers in the Western Cape. Mowing may also play a role in arable systems when hay crops are grown.
Chapter 4: Integrated crop-livestock rotations	Integrating grazed forage phases into crop rotations allows herbicide use to be reduced.	*Lolium* was less abundant and less dominant in rotations including grazed forage phases.	Integrating grazed forage phases into a rotation increases weed diversity both within fields and between fields.	Integrating sheep into arable crop rotations is already widely practiced in the Western Cape. Some vineyards also use sheep to graze in winter.
Chapter 5: Diverse cover crop mixes	Competitive cover crops can suppress weeds.	*Lolium* is suppressed alongside other weeds by competitive cover crops.	Competitive cover crops that reduce overall weed biomass may increase the diversity of the remaining weeds.	There are several competitive cereal and brassica cover crop species available in the Western Cape, but identifying or breeding competitive legume species would be beneficial for using cover crops to manage weeds in arable systems.

productivity and to the wider environment. Studies such as these, in combination with the findings of Chapter 3, suggest that perhaps herbicides result in yield benefits when first used, but in the long term their effect of eliminating the positive functions of weeds may result in agroecosystem degradation, a lower overall yield potential, and lower provision of ecosystem services to the wider environment and to society.

Regardless of the benefits of reducing herbicide use, however, measures do need to be in place to allow farmers to limit the negative impacts of weeds, given that uncontrolled weeds can substantially reduce yields (Oerke 2006). In Chapter 3, mowing offered a suitable alternative to herbicide use. However, this is less practical in arable cropping systems, and so Chapters 4 and 5 explored enhancing a) crop rotation and b) competitive crops as alternatives to herbicide use. Chapter 4 identified that rotations maximising management diversity between years can reduce the need for herbicides in weed management, and the findings of Chapter 5 suggest that crop species that produce a lot of biomass rapidly are more competitive for resources and thus more effective at weed suppression.

Despite these promising findings, it would be optimistic to suggest that either of these options could entirely replace herbicides at this stage. For example, in Chapter 4 it seems that the contrasting selection pressures between herbicides and grazing were the key to improving weed management in these systems, as other studies have not found grazing alone to be an effective weed management tool (Miller et al 2015, Lehnhoff et al 2017). Therefore, whilst integrating livestock into crop rotations can reduce herbicide use, it would not eliminate the need for herbicides in the absence of other tools or techniques that impose a selection pressure on weeds that differs from that of grazing. However, a reduction in herbicide use is still a step forward, as Davis et al (2012) demonstrated that diverse crop rotations posed a substantially lower potential toxicity to freshwater ecosystems due to reduced herbicide use. Increasing crop and management diversity for weed management also has benefits for other aspects of agroecosystem sustainability: in Chapter 4, grazed diverse rotations had a higher weed diversity and high cash crop yields, and also tended to be more profitable for farmers in the long-term than crop-only systems (Basson 2017). Grazing may also play a role in vineyard and orchard floor management. It may apply a similar filtering effect on weeds as mowing (McKenzie et al 2016), and thus Chapter 3's finding that mowing promoted more beneficial weed communities in vineyards may also apply to grazing. A recent study in New Zealand indicated that winter grazing by sheep reduced requirements to mow or spray herbicides in vineyards without damage to vines, and thus had both positive economic and positive environmental outcomes (Niles et al 2018).

An alternative weed management tool to both herbicides and grazing under conservation agriculture practices is the use of competitive cover crops (Chauhan et al 2012). In South Africa's winter rainfall region, cover crops can be used in both arable systems and as a floor cover in orchards and vineyards. Although the cover crop study in Chapter 5 of this thesis was conducted in arable systems, the ecological relationships identified also applicable to designing competitive cover crop mixes for vineyards and orchards. The key finding of Chapter 5 was the need to assemble cover crop mixes from productive species that are capable of rapid growth and thus able to sequester resources away from weeds early in the season. In practice, the most competitive cover crops currently available in South Africa's winter rainfall region are difficult to integrate into small grain rotations, given that competitive species tend to be either cereals or brassicas, and so risk bridging diseases between wheat and barley or canola cash crops. The utility of cover crops for weed management in these farming systems could thus be substantially improved through breeding or introducing productive legumes, or species from other plant families. However, this is not a problem in vineyards, where triticale and oats are both popular cover crop species.

Most previous work on cover crops in South Africa has integrated their use with that of herbicides for effective weed management, which somewhat undermines the potential of cover crops to reduce environmental impacts and to counter herbicide resistance. For instance, Fourie (2011) identified that both single species and diverse cover crops contribute to improved soil health and weed suppression in vineyards, but the best effects are achieved by terminating the cover crops with herbicides at vine budbreak to avoid competition with grapevines. Likewise, in small grain systems cover crops are typically sprayed off before seed-set, to prevent the cover crops from becoming a weed in the subsequent cash crop. However, current research investigating the utilisation of cover crops for grazing or mowing for hay may offer possibilities to suppress cover crops and any weeds amongst them sufficiently at the end of the season to prevent regeneration and seed-set (Strauss, J. and Smit, E. pers. comm.). In the cover crop trials described in Chapter 5, some cover crop species were observed to germinate amongst the cash crops the following year, and the potential threat of these to cash crop yield was not assessed. Achieving successful non-chemical cover crop termination currently poses a challenge to their use in sustainable weed management, but efforts to overcome this are underway (Wortman et al 2012, Wallace et al 2017, McKenzie et al 2017).

Overall, this thesis offers evidence that several measures can be successfully integrated into no-till arable systems to reduce reliance on herbicides. So far, these measures do not seem able to entirely eliminate the need for herbicides in small grain arable systems, but they are a step in that direction. Some future research is planned to further develop the effectiveness of some of the measures explored. For example, a new long-term trial commenced on Langgewens Research Farm in 2016 to explore whether further increasing crop and management diversity has further benefits in terms of reducing the inputs needed to suppress weeds and pests, and to maintain the required soil nutrient levels. This trial contains rotations with up to ten phases (Strauss, J. pers. comm.) and so conclusive results will not be available until at least 2026. Diverse cover crop mixes are also being further tested within this trial (Strauss, J. and Smit, E., pers. comm.).

In vineyards, the two organic vineyards included in Chapter 3 that avoided soil tillage demonstrated that mowing can be used as a main tool to achieve organic no-till weed management, and that this may result in weed community that provides more ecosystem services both to the farm and to wider biodiversity. However, comments from the vineyard managers suggested that weed management in such systems remained difficult, and that they occasionally needed to resort to labour-intensive hand-pulling of problematic weeds (pers. comm.). This suggests that more feasible alternatives in addition to mowing, tillage and herbicides would further improve weed management in vineyards.

Specific measures to reduce the dominance of herbicide-resistant Lolium *spp.*

Lolium is considered a problematic weed in South Africa's winter rainfall region due to its competitiveness with crops and capacity to reach high population levels in no-till systems: it is a relatively 'fast' species with herbicide tolerance traits. As indicated by both Chapters 3 and 4, replacing high herbicide use with either grazing or mowing in at least some years is therefore an effective way to reduce *Lolium* populations. These apply pressures to which *Lolium* is not so well adapted. A judicious amount of shallow tillage may also be applicable in some farming systems, compromising a small amount of soil disturbance for the potential benefit of suppressing small-seeded *Lolium* through seed burial (see Chapter 3). There is also some evidence that occasional tillage may be preferable to frequent herbicide use for soil conservation and health (Keesstra et al 2016). The effect of strategic minimum tillage once every few years with a harrow on weeds is currently under investigation at a separate long-term trial on Langgewens Research Farm (Tshuma, F. pers. comm).

Lolium's seemingly irrepressible productivity and capacity for adaptation also raises the question of whether it could be utilised rather than simply controlled. *L. rigidum,* probably the main component of most of the hybrid species in the winter rainfall region (Ferreira et al 2015), is not of particularly high forage value compared to other *Lolium* species, but does no harm as a contribution to the diet of sheep. When mown in vineyards, a lush growth of *Lolium* can be converted into a thick mulch for soil protection and further weed suppression; the challenge would just be to manage *Lolium* at the right time to avoid periods of critical competition with the vines. Various *Lolium* species are also used as cover crops in other parts of the world (e.g. Cotswolds Seeds 2018) and are valued for their productivity and dense root systems to improve soil quality. Thus, if ways can be found to increase the resilience of agroecosystems to the negative impacts of weeds, there would be no reason not to value *Lolium* as a useful member of a healthy weed community.

Using weeds to promote biodiversity

Given that agriculture occupies the vast majority of lowland areas in South Africa's winter rainfall region, a potentially substantial contribution could be made to restoring native biodiversity and associated ecosystem functions if agricultural landscapes could be converted to more hospitable habitats for native species (Gaigher and Samways 2010). In other parts of the world, the seeds provided by annual weed species are critical to sustaining farmland bird, small mammal, and arthropod communities (Marshall et el 2003, Gurr et al 2003, Blaix et al 2018). It is therefore plausible that increasing the diversity and abundance of native species that occur as weeds on farms, in combination with the restoration of more complex native habitats along fence lines and on marginal land, could serve to sustain some of the Western Cape's unique assemblage of species. However, it would be useful to confirm the extent to which different weeds support biodiversity in this region, and indeed worldwide, as the relationship is recognised to be important but is not yet well studied (Bàrberi et al 2010, Gaba et al 2017, Blaix et al 2018). In South Africa's winter rainfall region, it would be particularly relevant to explore native weeds and their relationships with other native wildlife, given that few native weeds were encountered in vineyards throughout this study, and even fewer in the trials in field cropping systems. Research that explores whether it is possible to sustain more native weeds, and how to achieve this, may be valuable in supporting the Western Cape's famously endemic and diverse flora, as well as other native wildlife that depends upon these plants.

Some have argued that a more effective strategy for biodiversity conservation is to focus on intensifying agricultural productivity so that sufficient food is produced on less land, and more land can be set aside for conservation. This is the concept of 'land-sparing', which is often contrasted against 'land-sharing' where conservation is achieved by managing agricultural landscapes to support biodiversity (Kremen 2015). The paradigm of 'land-sparing' is supported by several studies that highlight the existence of many species that cannot survive even under mild agricultural pressures (Phalan et al 2011, Egan and Mortensen 2012), and so it is necessary to conserve pristine habitats for these species. However, there is no reason not to seek increases in agricultural productivity through methods that *also* increase on-farm biodiversity. The findings of this thesis agree with those authors who argue that the best way to intensify agriculture is in fact to embrace 'wildlife-friendly' or 'land-sharing' practices (Chappell and LaValle 2011, Pywell et al 2011, Kremen 2015). Specifically, farming practices that conserved weed diversity through the use of softer and more diverse management (i.e. mowing, grazing, and crop rotation) were also found to result in better agronomic outcomes (reduced competition with crops, reduced input use, sustained yields). 'Land-sharing' is embodied by ecological intensification: work with nature, not against it, to enhance biodiversity and ecological functioning for sustained productivity.

Future directions to increase resilience to weeds in South Africa's winter rainfall region

The results of the three practical chapters of this thesis can be combined to identify some potential improvements to weed management practices in South Africa's winter rainfall region, as well as future research needs to further increase resilience to weeds. Taken together, the findings of Chapters 4 and 5 suggest that an optimal four-year rotation for small grain systems with integrated livestock, and using commonly cultivated crops, would be:

year 1: wheat
year 2: medic forage with intersown cereal cover crops
year 3: canola
year 4: medic forage with intersown brassica cover crops

This is a minor alteration to the best performing rotation system from the long-term trial described in Chapter 4, with competitive cover crops intersown amongst the medics to improve weed suppression. Intersowing competitive cover crops would be expected to be particularly effective in annual pasture systems where sheep are kept aside on saltbush forage while the pastures establish (see Chapter 4), as they would present competition to weeds in periods when grazing is absent and when legumes such as medics and clovers are typically less productive (as observed from the slow early-season legume growth in Chapter 5). Cereals are grown before the canola year and brassicas before the wheat year to avoid problems with promoting cash crop diseases. These competitive cover crops could also be grazed to contribute to livestock production, and current ongoing research suggests that mixed species forages with a legume base provide similar soil nutrient benefits to a cover crop that is not utilised. These mixed forages also appear capable of sustaining relatively high stocking rates (Smit, E. pers. comm).

Research into allelopathy against weeds by crops may also increase potential to design cover crop mixes and crop rotations that better suppress weeds. In other parts of the world, it has been shown that crop allelopathy can substantially reduce weed abundance (Jabran at el 2015, Kunz et al 2016), and that some cover crops produce allelochemicals that are only effective against certain plants (Dhima et al 2006), potentially enabling them to be used in the same manner as selective herbicides. There is evidence to suggest that barrel medic *(Medicago truncatula)* and lupins *(Lupinus albus)* have allelopathic effects in arable systems of the winter rainfall region (Ferreira and Reinhardt 2010), which may partly explain the benefits of crop diversity in rotation systems observed in Chapter 4.

In vineyards and orchards, in comparison with arable farms, the lower competition pressure between grapevines and herbaceous weeds means that the focus of weed management on limiting weed abundance can be reduced in favour of promoting the positive functions of weeds, such as protecting soil and providing habitat to beneficial insects. Reducing the intensity of weed control actions also appears to reduce the competitive pressure imposed by weeds against grapevines through reducing selection pressure for problematic species. It would be useful to explore this further; the study presented in Chapter 3 can only show correlation, and trials of altering management to intentionally shift weed communities would provide farmers with more concrete information to actively manage their weed communities for positive functions. Increasing temporal management diversity as well as reducing intensity may also play a role in vineyards; unfortunately, the data were not collected in a way that allowed this to be assessed in Chapter 3, but the findings from Chapter 4 suggest it would act to limit weed abundance to promote diversity. Temporal management diversity could be achieved in perennial crops through varying floor management actions between years (e.g. mowing, grazing, and cover cropping). Further research would be useful to explore if and how ‘divergent selection pressure’ and ‘directional selection pressure’ can be combined to optimise weed management, as possibilities for divergence are reduced by choosing management actions that would select for specific sets of traits.

In addition to the various options described so far, there are several theoretical possibilities for more sustainable weed management that were identified in the literature review (Chapter 2) but not addressed in any of the practical chapters. For example, intercropping is not currently widely practiced in field crop systems in South Africa’s winter rainfall region, but techniques developed in similar regions of the world may be applicable, such as Australian ‘peaola’ systems where canola and peas are grown together (Fletcher et al 2017). Peas fix nitrogen and cover soil between canola plants, and the difference in seed size between the crop types allows for easy post-harvest seed sorting. Anecdotal evidence suggests some farmers in South Africa’s winter rainfall region have begun to experiment with vetch-cereal mixes, which apparently also allow for easy post-harvest separation (Smit, E. pers. comm.).

6.4 Implications for agricultural sustainability in South Africa’s winter rainfall region

Potential contributions to sustainability

Several of the weed management options explored in this thesis are ‘win-win’ solutions that improve environmental sustainability as well as long-term farm yields and profits, and thus increase the capacity of agriculture in South Africa’s winter rainfall region to remain within the ‘safe and just space for humanity’. The major contributions to agricultural sustainability of these weed management practices are summarised in Table 6.3, and primarily result from their role in reducing farm input requirements through enhancing on-farm ecological functioning. Many of these ecological functions are not only beneficial for the sustainability of weed management, but are synergistic with other aspects of agricultural sustainability, such as crop diversity that suppresses diseases as well as weeds and thus promotes higher yields, integrated legumes that reduce the need for fertiliser inputs, and increased weed diversity that can increase biodiversity at other trophic levels. Reducing inputs and enhancing ecosystem function not only mitigates the environmental costs associated with most agrichemicals and with biodiversity loss, but also contributes to creating agricultural systems that achieve Raworth's 'social foundation' (Figure 1.1). Reducing inputs reduces the exposure of farmers to health risks and market vulnerabilities, and diverse systems tend to produce more reliable yields and be more resilient to both environmental and financial perturbations (Cabell and Oelofse 2012, Tscharntke et al 2012).

As explored in Section 3.1.1, the findings of this thesis specifically have potential to reduce reliance on herbicides through increasing the effectiveness of other techniques including crop rotation and competitive cover crops, and highlighting the benefits of 'softer' techniques in retaining the positive functions of weeds whilst still limiting their abundance to acceptable levels. Reductions in herbicide use can be expected to reduce the risks of pollution and human health impacts associated with weed management (Davis et al 2012) and avoid issues with herbicide resistance (Shaner and Beckie 2013). Softer management practices that retain weeds in agricultural landscapes can contribute to biodiversity conservation and soil quality (Keestra et al 2016, Blaix et al 2018). These options are also consistent with no-till practices, thus enabling farmers in the region to continue avoiding the soil erosion problems associated with regular tillage, and to promote soil carbon capture.

These synergies illustrate that taking an ecological intensification approach, and thus needing to work within ecological constraints, tends to favour the ecological functioning of the whole agroecosystem. In contrast, the intensive use of tools such as herbicides and tillage, which apply unnaturally high levels of toxicity or disturbance to a system, tend to result the in degradation of other aspects of the system. Attempting to create these unnatural conditions also appears to result in farmers needing to constantly work against natural processes, such as the colonisation of areas with available resources by weeds (Smith 2015), or the adaptation of weeds to consistent selection pressure (Neve et al 2009). Ecological intensification offers opportunities to instead direct such processes toward productivity and other ecosystem services, for example by selecting for weeds that support biodiversity (Chapter 3), by using weeds promoted by cash crops as a component of forage for livestock (Chapter 4), or by planting crops that are more able to utilise all available resources (Chapter 5).

Dissemination and expected impact of findings in South Africa's winter rainfall region

As noted in the introduction, the topics of the practical chapters in this thesis were chosen to be of current interest to local farmers and researchers, to increase adoption of useful findings by farmers and maximise opportunities for collaboration with local researchers. Findings from this thesis have been and continue to be disseminated through farmers' days, farmers' magazines and national scientific conferences (Appendix 2), both of which are avenues that can reach a wide audience in the region. As explored in Section 1.3.1, previous change in farming practices in the region appears to be widely driven by farmer-led 'innovation platforms', or groups who gather regularly to share information and experiences, and sometimes conduct on-farm trials (Smith et al 2017). Farmers who belong to such groups are frequent attendants of farmers days, which are often organised through or in cooperation with the platforms. It can be deduced from their effort to attend the farmers days and membership of innovation platforms that such farmers are likely to be early adopters (Läpple and Van Rensburg 2011, Diederen et al 2015), or those who are more open to taking up new tools and practices. Given that the 'neighbour effect' and farmers' social networks further influence adoption (Läpple and Van Rensburg 2011, Ward and Pede 2014), it is expected that early adopters of useful findings will spread these to those around them. Given that conservation agriculture practices were rare in the winter rainfall region in the 1990s but are now nearly ubiquitous, and that this spread appears to have been largely farmer-led (Smith et al 2017), there is reason to expect that findings from this thesis that are presented at farmers' days and in farmers' magazines, and that are perceived by farmers to be useful, will make their way into common regional practices.

Table 6.2: Summary of potential contributions to sustainability if the findings from this thesis are implemented in farm practice, in the context of Raworth's (2012) conceptualisation of sustainability as the 'safe and just space for humanity' between the 'social foundation' of human needs and wellbeing and the 'environmental ceiling' of the planetary biophysical boundaries (Rockström et al 2009). These points are discussed in greater detail within each chapter and in the main text of this discussion chapter.

	Avoid pressure on environmental ceiling	**Meet human needs and support wellbeing**
Chapter 2: Ecological strategies for resilience to weeds (review)	• Provides a conceptual basis for weed management strategies that rely less on environmentally damaging inputs, that promote weed diversity, and that are compatible with other necessities for agricultural sustainability	• Provides a conceptual basis for weed management that would safeguard the long-term productivity of agroecosystems • Identifies several potential options for sustainable weed management that would have additional benefits to reduce crop disease, build soil health, diversify farm production and reduce input expenses, thus increasing overall agroecosystem resilience to a variety of potential perturbations • Identifies options for weed management that avoid chemical health risks to farm workers, consumers, and water supplies
Chapter 3: Management to minimise competition/ biodiversity trade-off	• Indicates that weeds can be managed to optimise desirable traits whilst minimising problematic traits, thus allowing a greater amount of weeds to be retained to provide positive functions with minimal impacts on yield • Shows that weeds can be managed effectively in vineyards with reduced herbicides and tillage Shows that mowing can increase weed diversity and the cover of native weed species, and could thus contribute to supporting native biodiversity	• Demonstrates that vineyard weeds can be managed effectively without herbicides, thus reducing health risks • If mowing results in less competitive weeds, then irrigation and fertiliser requirements (and their costs) may be reduced
Chapter 4: Integrated crop-livestock rotations	• Demonstrated that integrating livestock into diverse crop rotations can sustain yield in no-till systems whilst reducing herbicide and fertiliser use • This can also promote weed diversity and would thus be expected to increase support to wider biodiversity	• Integrating livestock into diverse rotations sustains yields with reduced environmental impacts • It also reduces input costs and diversifies production, which makes farms more profitable and more resilient Reduces health risks associated with herbicide use
Chapter 5: Diverse cover crop mixes	• Increased understanding of cover crop mix design so that farmers can be provided with information that allows them to use cover crops more effectively in weed management, and thus encourage the continued use of cover crops to provide a variety of ecosystem functions that can reduce input requirements • Increased understanding of how to use cover crops effectively in weed management so they can contribute to reducing herbicide use and so reduce environmental impacts	• Increased understanding of how to design cover crop mixes to minimise input requirements and maximise their contributions to cash crop yields • Increased understanding of how to use cover crops effectively so they can contribute to reducing herbicide use, thus reducing health risks associated with herbicides

Much of the research contained in this thesis comprised evidence to support the continued use of, or small modifications to, common practices in South Africa’s winter rainfall region. For example, crop rotation is a typical practice, as is integrating livestock on grazed forages. However, if the results presented here can sway the opinion of farmers who have been considering livestock or increased crop diversity but not yet made the change, then this would have a beneficial effect on reducing herbicide and fertiliser use and promoting weed diversity in the region. Similarly, farmers who have had problems with weeds in their cover crops may be able to use the information presented here to manage these more effectively, and thus be more likely to continue the use of cover crops, which have multiple sustainability benefits. It is also hoped that the results from the vineyard study will provide some inspiration to those weed farmers struggling with multiple herbicide-resistant *Lolium* spp. to trial reductions in herbicide use in favour of mowing.

As discussed in previous sections, much of the research presented here would benefit from additional research to enhance the outcomes or fine-tune some practical issues, such as the need for competitive cover crops that are neither brassicas nor cereals. Whilst some research could certainly be conducted by interested ‘early adopter’ farmers themselves through on-farm trials, it is expected that much of this work will be continued by the researchers with whom the author collaborated on the practical chapters of this thesis. Work was undertaken alongside researchers from the Department of Agronomy at Stellenbosch University (SU) and the Western Cape Government Department of Agriculture (WCGDA), who lead much agronomic research in the winter rainfall region. In particular, the WCGDA run the regional government research farms, upon which the majority of practical trials are conducted, particularly long-term trials. These relationships with local researchers are also valuable due to their connections to the various agronomic research boards that provide support to, and thus can influence, both farmer innovation platforms and academic research projects. Whilst researchers at both the WCGDA and SU were already motivated to include sustainability as an objective in much of their work, it is hoped that the author’s ecological approach to the studies presented in this thesis was able to demonstrate the wide range of possibilities for ecological intensification, and the value in making this approach a greater element of their work. The informal feedback received by the author suggests that this is the case. Likewise, it was valuable for the author to collaborate with agronomists, to ensure that her ideas for ecological intensification could be constrained to actions that actually had practical potential for regional farming systems.

Involving farmers in research design can also result in research that is more relevant to farmers and thus increase farmer adoption of findings (Snapp et al 2003). Such an approach was not taken in this thesis, given that testing the translation of ecological theory to agricultural practice is not necessarily something farmers would want to invest time or money participating in, or risk reduced yields for, until there is some evidence that specific ideas and practices can be effective. However, refining these more promising practices in cooperation with farmers, using tactics such as on-farm participatory trials by members of regional farmer innovation platforms, would be an effective way to ensure the techniques are optimally adapted to local conditions (Payne et al 2016). Barriers to adoption could also be assessed, in terms of agronomic, economic or socio-political constraints, or adverse farmer perceptions (Doohan et al 2010, Liebmann et al 2016). Participatory research would be useful approach to refine the implementation and encourage the adoption of the ecological intensification practices explored in this thesis.

6.5 Ecological intensification as the future of weed management

This thesis has so far demonstrated that an ecological intensification approach to weed management can contribute to reducing unsustainable practices such as intensive herbicide and tillage use through harnessing ecological functions that act to limit weed abundance and to promote weed diversity. Such ecological functions confer resilience to the negative impacts of weeds by reducing opportunities for weeds to become problematic, for example by reducing resource availability and by increasing the variability of conditions experienced by weeds. This avoids problems associated with conventional weed management, in which weed removal can simply create opportunities for new weeds (Smith 2015), where farmers find themselves trapped in a ‘co-evolutionary arms race’ between weeds and weed control (Neve et al 2009), and where the methods used to control weeds pose risks to both the natural environment and to human health (see Chapters 1 and 2).

Given these critical advantages of taking an ecological intensification approach to weed management, it is remarkable that many scientists in the field of weed research remain committed to an agenda based on modifications to herbicide and mechanical technology (Harker and O’Donovan 2013, Shaner and Beckie 2013, Bajwa et al 2015, Westwood et al 2018). Further research on herbicides seems unlikely to offer substantial benefits in terms of weed management, but likely to continue to carry risks to environmental and human health. These risks largely result from the fact that herbicides are synthetic and thus entirely novel to Earth’s ecosystems, or that they are applied in concentrations much greater that would normally occur in natural ecosystems. Consequently, relatively few species across all taxa from the microbes to megafauna, and including humans, are adapted to thrive in the presence of such chemicals. However, the consistent use of herbicides over past decades has promoted adaptation amongst the one class of organisms that we would rather did not thrive: the weeds themselves (Neve et al 2009).

The discovery of new herbicide modes of action has stagnated, with none developed since the early 1990s. Westwood et al (2018) predict that another four modes of action may be discovered by 2050, and whilst each of these may be effective for a short time following discovery, this discovery rate would not be sufficient to avoid herbicide resistance. Four new modes of action before 2050 equates to one new mode of action every eight years (and may be a highly optimistic estimate given that zero new modes of action have been discovered in the last 25 years). Given that traits leading to avoidance of the harvest weed seed destructor emerged within two years of the technology becoming widespread (Ashworth et al 2015), avoiding resistance for eight years seems highly unlikely. Herbicide resistance does not necessarily carry a fitness cost in herbicide-free environments (Vila-Aiub et al 2014), and so there is also no guarantee that resistance to older herbicides will decline if they are temporarily replaced with newer chemicals. It is also apparent that some weeds can become tolerant of all herbicides, regardless of the type of active chemical. A key example of this is *Lolium,* with its waxy cuticles and variable germination times that reduce the amount of chemical that each plant comes into contact with. These not only increase the potential that *Lolium* will rapidly develop resistance to new modes of action, but also reduce the capacity of a new chemical treatment to achieve effective weed control.

Overall, the slim chance of developing a new herbicide that can achieve effective weed control in the long-run does not seem worth the potential harm to human and ecosystem health, nor worth the opportunity cost of dedicating the research effort and funding to more promising avenues for sustainable weed management. Herbicides are currently necessary tools to manage weeds in today's simplified farming systems, but they are also dangerous tools with a finite utility and alternatives urgently need to be found.

Many other 'techno-fixes' to weed management proposed in recent weed reviews such as those by Westwood et al (2018), Bhajwa et al (2017), and Shaner and Beckie (2014), may run into similar problems as herbicides. Genetic engineering or gene editing, for example, also runs the risk of altering ecosystems in unforeseen ways by creating novel organisms that may respond to their environment in unpredictable ways. Whilst this risk does not necessarily outweigh the other potential contributions of genetically modified organisms to sustainability, it does emphasise that the interactions of such tools with both agroecosystems and natural ecosystems need to be considered extremely thoroughly in order to avoid long-term negative impacts. This has been demonstrated by the 'Round-Up

Ready' crops, which were released with the promise of reducing overall herbicide use, but within two decades have resulted in an overall increase in herbicide use (Bonny 2016).

The fundamental drawback of 'techno-fixes' for weed management, be they chemical or mechanical or genetic, is the tendency to apply them to meet the narrow goal of reducing weed biomass. The interactions between weeds, weed management and agroecosystems at a systems level are not considered. As a consequence, these 'techno-fixes' often impact other aspects of farm productivity or sustainability, such as herbicides interfering with microbial community functioning, or tillage causing soil organic matter loss. In contrast, designing ecological weed management strategies in the context of the whole agroecosystem facilitates the implementation of strategies that address the multiple goals needed to achieve sustainability. For example, replacing synthetic fertilisers with grazed legume rotations has potential to suppress weeds through increasing management diversity and reducing resource availability (Chapters 2 and 4), and can also minimise environmental harm and sustain productivity through reducing herbicide use, fertiliser use, freshwater pollution, nitrate leaching, the loss of soil organic matter, and carbon emissions (Drinkwater et al 1998, Crews and Peoples 2004, Davis et al 2012).

Given the disadvantages of conventional weed management and of 'techno-fixes' in comparison with the benefits offered by ecological intensification, it is clear in which direction we should steer the future of weed science. However, the ecological intensification of weed management is not a simple task and much work will be required to implement it successfully. Not every promising ecological theory will turn out to function as expected in the field (e.g. cover crop diversity in Chapter 5), and every ecologically-based management technique will need to be adapted to local environmental conditions, farming systems and available tools. To do this effectively, we will need to work more closely with one another (Ward et al 2014, Neve et al 2018), and also with farmers and practitioners whose local and traditional knowledge can provide insight for locally effective solutions

(Jordan et al 2016). All of this, however, should present an exciting challenge to weed scientists, agronomists and ecologists. Pursuing the ecological intensification of weed management will allow us to increase the diversity of ideas, theories, tools, practices and people that we work with, and to link these together in novel ways to design resilient and sustainable farming systems.

6.6 Conclusions

This thesis has presented ecological intensification as an approach to weed management that could contribute to shifting agriculture into the ‘safe and just space for humanity’ of sustainability, between meeting our needs and avoiding impacts on the integrity of Earth’s life-supporting ecosystems. It demonstrated the process of drawing together a wide range of ecological theories that could potentially be harnessed to limit the negative functions of weeds but promote their positive functions, then tested the practical implementation of some of these in South Africa’s winter rainfall region. This approach allowed simultaneous advances to be made in weed ecology and in identifying locally relevant practices that can contribute to sustainable weed management. Specifically, it was found that practices that could increase the diversity of filters applied to weed communities while decreasing filter strength, and that could reduce resource availability, could confer agroecosystem resilience to weeds. Approaches that can achieve this in South Africa’s winter rainfall region include reducing herbicide use in favour of mowing or grazing, implementing diverse crop rotations with diverse management practices, and using highly productive crops to compete with weeds for resources. Much work remains to be done to improve the efficacy of these practices, as well as to test the range of other possibilities identified in Chapter 2 that may further contribute to increasing the sustainability of weed management. Overall however, the findings of this thesis suggest that ecological intensification offers a promising direction for future weed management to achieve agricultural sustainability, both in South Africa’s winter rainfall region and around the world. Weed researchers can assist farmers in this challenge by drawing on global advances in weed ecology to design and test locally appropriate weed management techniques and strategies.

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APPENDIX 1: MODEL SPECIFICATIONS

Regression models were employed in Chapters 3-5 to explore how farm management and environmental variables were related to weed response variables. Due to nested sampling designs and repeated measures, mixed effects models were used in Chapters 3 and 4 (Bolker et al 2008, Zuur et al 2009). The need for these was avoided in Chapter 5 by standardising all variables to the mean of each replicated block, which removed any inherent differences in the values of each variable between sites and years (e.g. differences in productivity related to rainfall, soil quality, historical site management etc).

In Chapter 3, the mixed effects models included the vineyard, block and quadrat were included as random effects given that each sampling unit was a split quadrat, of which four were nested in each block, and two blocks were nested in each vineyard. The model structure was thus:

response ~ fixed effects [explanatory variables] + random effects [quadrat/block/vineyard] + error

where “ / ” indicates that the previous variable is nested in the subsequent variable, and the ‘explanatory variables’ were the management or environmental variables included in the model, as described in Chapter 3.

In Chapter 4, samples were collected from the same plots each year, and thus inherent differences between plots may have influenced the observations. Plots were not laid out in a blocked design and so differences in each individual plot were taken into account:

response ~ fixed effects [explanatory variables] + random effects [plot] + error where ‘explanatory variables’ were either rotation system and period, or the management variables and period, as indicated in Chapter 4.

In Chapter 5, generalised linear models were used with fixed effects only (due to the standardisation procedure used):

response ~ fixed effects [explanatory variables] + error

Model distributions (e.g. Normal, Poisson, binomial) were selected as described in each chapter to avoid any trends or heteroscedasticity in the residuals, and significance tests for parameters and pairwise comparisons were selected for reasons and criteria outlined in Bolker et al (2009).

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APPENDIX 2: LOCAL DISSEMINATION OF FINDINGS

A2.1 National agricultural conferences

Annual Congress of the Grassland Society of Southern Africa (2017): MacLaren, C., Bennett, J., Swanepoel, P., Wright, J., & Dehnen-Schmutz, K. *Designing diverse forage crops for weed suppression* [oral presentation]. Hoedspruit, South Africa.

Combined Congress of the South African Crop Production, Weed Science, Soil Science and Horticultural Sciences Societies (2017): MacLaren, C., Bennett, J., Wright, J. & Dehnen-Schmutz, K. *Functional traits for strategic weed management in vineyards* [oral presentation]. Klein Kariba, South Africa.

Annual Congress of the Grassland Society of Southern Africa, 2016: MacLaren, C., Bennett, J., Swanepoel, P., Strauss, J., Wright, J., & Dehnen-Schmutz, K. *Designing diverse forage crops for weed suppression* [poster]. Wilderness, South Africa.

A2.2 Popular articles

MacLaren, C. *in press*: Integrating sheep into diverse crop rotations can suppress weeds, save money, and protect the environment. *Landbou Weekblad (Farmers Weekly).* [will be published in Afrikaans]

A2.3 Field talks at local farmers' days

Langgewens Research Farm Walk & Talk (2018): Integrating sheep into diverse crop rotations can suppress weeds, save money, and protect the environment.

Langgewens Research Farm Green Tour (2017): designing cover crop mixes for weed suppression (Figure A2.1).

A2.4 Local university field trips

Langgewens Research Farm field trips (2017 and 2018) for final year students completing a Bachelor of Science in agricultural sciences at Stellenbosch University: presentation of trial design and findings on both integrating livestock into diverse crop rotations (Chapter 4) and on using cover crops for weed suppression (Chapter 5).

Figure A2.1: The author explaining her cover crop trials at the Langgewens Research Farm 2017 Green Tour.