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Review

Integrating associational resistance into arable weed management

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ABSTRACT

This review considers how natural weedy vegetation affects herbivory in arable crops, and how such 'associational effects' may be set against other factors affecting crop yield that are better understood, such as competition for resources. Natural vegetation may reduce or increase herbivory by three broad categories of mechanisms: (1) directly, by altering the behaviour of herbivores, (2) indirectly by altering the behaviour of natural enemies or (3) indirectly by altering crop plants' growth and physiology. The first category includes natural vegetation diverting herbivores away from crop plants, which appears to be the most beneficial effect, but this is sensitive to the spatial scales at which herbivores forage. There is little evidence that mechanisms in the second category significantly affect crop performance. The viability of crops is critically dependent on the dynamics of plant–plant interactions (the third category) and their interactions with associational effects. While few published studies demonstrate the potential for weedy vegetation to improve crop yields, there is clear scope for optimising weed management with regard to economics, pesticide use and conservation.

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1. Introduction

Arable weeds often interfere with crop production by competing for resources (Lampkin, 2002), but natural vegetation that colonises crop stands can also reduce herbivory. Associational resistance occurs if plants growing in more-diverse stands of vegetation suffer less herbivory (Andow, 1991a). It has been scientifically investigated since the 1960s (van Emden, 1965; Smith, 1969) and may be attributed to a wide range of ecological processes. However, little work has been done on interactions between associational resistance and competitive interference, perhaps because it is difficult to disentangle these effects experimentally. The effects of diversifying field vegetation on crop yields have been reviewed by Andow (1991b) and Poveda et al. (2008), but improved understanding of where associational resistance occurs (Barbosa et al., 2009), of the economics of plant defences (Agrawal, 2011) and of the conservation value of agriculture (Jackson et al., 2007) together highlight the need to explore how natural vegetation can be managed to maximise associational resistance and minimise competition.

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This paper considers the range of mechanisms that may link crop yield to the presence of natural vegetation that develops in fields and field margins. This focus excludes intercropping (Vandermeer, 1989), which normally concerns substitution of one crop type for another, although some of this literature is relevant. The conclusions should contribute to integrated pest management (Kogan, 1998), besides wide-ranging conservation and aesthetic benefits. The relative importance of different mechanisms for associational effects is considered first, followed by the question of how cropping systems may be manipulated to obtain more benefits from natural vegetation at lower cost.

2. Mechanisms for associational resistance and associational susceptibility

Two general hypotheses, first formulated by Root (1973), may explain reduced herbivory in more-diverse plant stands. The resource concentration hypothesis says that less-pure, less-dense or smaller stands of a herbivore's host plants are less attractive to herbivores and therefore suffer less damage, while the enemies hypothesis says that more complex habitats support more predators and parasitoids, leading to increased herbivore mortality. A third set of hypotheses involves plant quality (Theunissen, 1994), where physiological or morphological changes induced by neighbouring plants make focal plants more resistant or less attractive to herbivores. This phenomenon, also termed "bottom-up effects" (Hooks and Johnson, 2003), is closely linked with plant competition. Combined hypotheses may also be tested, such as resource concentration effects on root herbivores leading to plant-quality effects on above-ground herbivores (Moore et al., 2003), or plant-quality effects via natural enemies (Ninkovic and Pettersson, 2003).

Diversifying plant stands does not always reduce herbivore damage. In a recent meta-analysis, the presence of heterospecific neighbours was associated with increased and decreased damage to plants in similar numbers of cases; overall there was a significant reduction in herbivore abundance but not in plant damage (Barbosa et al., 2009). A review of arable studies found that pest pressure declined significantly in 52% of cases but increased in 12%, while crop yield increased significantly in 32% of cases but declined in 29% (Poveda et al., 2008). The phenomenon of increased herbivory in diversified plant stands is termed "associational susceptibility" (Brown and Ewel, 1987) and may be explained by another set of hypotheses concerning herbivore behaviour, natural enemy effects and plant quality effects.

For arable crops, associational resistance is best documented by entomological studies using sown companion plants (Andow, 1991b; Tonhasca and Byrne, 1994). The following three sections therefore combine ecological reasoning with evidence from several meta-analyses to explore the possible associational effects of additional natural vegetation on all kinds of herbivory. The aim is to identify the mechanisms that are most conducive to sustained yields by first considering herbivore behaviour, natural enemy effects and plant quality effects in turn, and then considering a conceptual model for multitrophic interactions and competition.

2.1. *Herbivore behaviour: density and distribution*

A large number of mechanisms have been proposed for direct effects of plant diversity on herbivores (e.g. Finch and Collier, 2000; Norris and Kogan, 2000; Hambäck and Beckerman, 2003; Barbosa et al., 2009). However, an important distinction should be made between effects on population density and on distribution. The combined effect of crop and non-crop plants may attract herbivores to a field, repel them from it or stimulate population growth or decline – affecting population densities. At the same time, the juxtaposition of different plant species, or of plant stands differing in composition, may lead to herbivores discriminating between the different qualities of habitats on offer – altering their distributions. The distinction is similar to the "coarse-grained" vs. "fine-grained" habitat distinction introduced by Levins and Macarthur (1966). The relative importance of these effects for herbivores and natural enemies will depend on their foraging behaviours and the spatial arrangement of crops, and may vary with different stages of life-cycles and foraging.

Herbivore densities can be affected by repulsive volatiles. In some cases herbivores may be repelled by non-host-plant volatiles – as, e.g., for ovipositing cabbage white *Pieris rapae* (Hern et al., 1996), though not for foraging cabbage root fly *Delia radicum* and onion root fly *D. antique* (Finch et al., 2003). Masking of host plant odours by other plants has been widely proposed but rarely demonstrated (but see Thiery and Visser, 1986), though it may be conceptually inseparable from repellence (Schroeder and Hilker, 2008). Such effects support the resource concentration hypothesis (Root, 1973) so long as non-crop plants are close enough to crop plants to prevent herbivores discriminating between emitting and non-emitting plants.

The resource concentration hypothesis may also be attributed to altered herbivore distributions. Non-crop seedlings can divert limited local populations of slugs away from crop seedlings among which they are interspersed (Cook et al., 1997; Frank and Barone, 1999; Brooks et al., 2005) – also described as a dilution effect. For specialist airborne insect herbivores, the appropriate/inappropriate landings theory (Finch and Collier, 2000) proposes that herbivores land indiscriminately on green surfaces once olfactory cues from a host plant are present; it has been supported in studies of cabbage and onion root flies, where foraging is disrupted by weeds covering bare soil and extending to at least 50% of the height of the crop (Finch and Collier, 2000). At the whole-field scale, strips of suitable "barrier" or "trap" vegetation bordering a crop can be effective for impeding invasion by aphids (Hooks and Fereres, 2006). The push–pull strategy (Shelton and Badenes-Perez, 2006; Cook et al., 2007) combines two elements: sacrificial crop stands, bordering or interspersed with a main crop, attract herbivores, while companion plants within the crop repel them (Khan et al., 2008). This may be the best approach for protecting crops from mammal herbivory (Bilenca et al., 2007), although it may be too species-dependent to work with natural vegetation.

Importantly, associational susceptibility may arise if weeds increase the density of herbivores by providing supplementary food resources or cover. For example, a palatable cover crop such as red clover may increase populations of generalist herbivores such as slugs (Vernava et al., 2004) – both by attracting individuals and by facilitating reproduction. Associational susceptibility could also result from altered herbivore distributions if herbivores were attracted to crop stands in proportion to the amount of vegetation cover, as they might be by a visual cue, and were then repelled from the non-crop vegetation onto the crop. Some evidence suggests that host plants in smaller patches suffer more herbivory (Hambäck et al., 2010). It is not clear whether additional vegetation would effectively fragment a crop into small patches for this purpose and the resource dilution hypothesis (Otway et al., 2005) needs further investigation for arable habitats.

2.2. *Enemies effects: a chain of hypotheses*

Meta-analyses of field experiments have found positive effects of habitat diversity on natural enemy abundances (Langellotto and Denno, 2004; Bianchi et al., 2006). However, an early review of agricultural studies found little evidence that natural enemies effectively reduce herbivory (Risch et al., 1983), and this conclusion was recently upheld (Jonsson et al., 2008). Moreover, studies com-