Ecology of wild oats

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Introduction

Ecology is about how organisms interact with their environment. The first observation one can make about the ecology of wild oats (*Avena* spp.) is that it must interact very well in order to be such a highly successful weed.

Given the central objective of this Co-operative Research Centre is to reduce the cost of weed control via a reduction in populations, this review will focus on those processes regulating population dynamics. Many possible topics have not been included in order to maintain this focus; crop competition being a notable omission, since this has been the subject of a separate Co-operative Research Centre workshop.

A convenient way to examine the features contributing to the success of wild oats is to partition its life cycle into life states (seed banks, seedlings, adults and seed set) and their respective probabilities of survival / growth (seed bank survivorship, seedling recruitment, plant survivorship, reproduction and dispersal), which are also referred to as transitional fluxes. Perhaps the greatest value of this approach is not just to describe the dynamics of a weed, but to determine the strengths and weaknesses of the life cycle processes. Better management techniques may then be devised by exploiting the weaknesses, although Cousens and Mortimer (1995) caution that current models may be too general to credibly achieve this objective.

Recruitment

Little attention has been devoted to understanding recruitment, which is a highly interactive process between seeds and the environment. We are far from being able to predict recruitment behaviour and our knowledge can be summed up by a few general statements. Annual rates of recruitment of up to 60% of the seed bank have been observed and periodicity of germination can fluctuate widely with seasons (Medd *et al.* unpublished data, Martin unpublished data).

Episodic germination leads to staggered recruitment of wild oats which varies among species. *Avena fatua* L. tends to germinate from autumn through to spring whereas *A. ludoviciana* Durieu., which responds to cooler temperatures, germinates in winter and early spring (Thurston 1961, Quail and Carter 1968). The latter authors further reported that a preponderance of *A. fatua* seeds germinated early in the season whereas most *A. ludoviciana* seeds germinated later, that this pattern varied for primary and secondary seeds, and that any seed is unlikely to germinate once temperatures exceed 20°C.

Seed dormancy is a key process controlling recruitment. The considerable inputs invested into understanding dormancy mechanisms in wild oats, have seemingly yielded little practical dividend (see Simpson 1992 for an overview). The ultimate weed management ambition of inducing mass stimulation of synchronous recruitment in order to purge seed banks, has to date met with little success. Control is sub-optimal because of protracted recruitment, since a single early application of any non-residual herbicide will give unsatisfactory control. We are no closer to solving these problems.

A further paramount consequence of dormancy is its role in seed longevity (persistence). Contrary to common belief, wild oat seeds are short-lived (see below) and under arable conditions only a small proportion of seeds survive for longer than three years. Seed bank flux rates are therefore high, with around 60–70% annual rates of loss (in addition to losses attributable to recruitment). Is this the real "Achilles' heel" of wild oats?

Seed production

Being annuals, wild oats depend on their seeds for survival, multiplication and invasion. Although mostly neglected, control should aim to minimize seed production and the number of seeds returned to the soil, since these add to the reservoir (or seed bank) from which subsequent infestations are recruited.

Seed production is usually expressed as a function of plant density, but since it is an outcome of competition it is also influenced by other factors such as time of emergence and crop density. The number of seeds produced per plant (fecundity) is a highly plastic, density-dependent parameter. In analysing data from the northern grain region, Medd (in press) estimated maximum fecundity to be around 225 seeds plant^{-1} at low plant density, and <50 seeds plant^{-1} for densities above 50 plants m^{-2}. Unsprayed plants tended to be the most fecund, and below about 40 plants m^{-2} the potential fecundity appeared to lack density dependence.

Further analysis by Medd (in press) showed that seed production by untreated plants ranged from 1000 to a peak of around 10 000 seeds m^{-2}. In herbicide-treated crops seed production was mostly less than for the untreated, with an apparent ceiling of around 5000, whilst the minimum rarely fell below 300 seeds m^{-2} for densities above 50 plants m^{-2}. Medd *et al.* (1995) described relationships for high, mean and low seed production using a rectangular hyperbolic model.

Apart from weed density, at least some of the considerable variation in seed production can be attributed to crop density. Radford *et al.* (1980) showed that whilst seed production was maximal at low crop densities, it declined as crop density increased, especially at low weed densities. These data support the generalization that herbicides fail to adequately control seed production (Wilson *et al.* 1974, Martin and McMillan 1984, Paterson 1977, Wilson 1979), as rarely was it brought below 100 seeds m^{-2}. A comparison of crop versus wild oats density dependence revealed that crop density above 75 plants m^{-2} stabilized seed production following treatment with herbicides to a maximum of about 200 seeds m^{-2}, irrespective of wild oat density. Although increasing crop density reduced wild oat seed production in untreated crops, seed production increased with higher weed densities. Where wild oats are controlled with herbicides, these findings indicate that more competitive crop cultivars are liable to have minimal impact on seed production.

Setting directions and strategies

The population size of annuals such as wild oats is the product of five main transitional parameters: seedling recruitment (germination and emergence); seedling survival to adulthood (survivorship); the number of seeds produced per adult (fecundity); the number of produced seeds entering the seed bank (seed rain) and; the chance of seeds surviving in the soil (seed carry over or persistence). Any one of these transitional fluxes may be regulated. However, since the advent of herbicides, weed control has concentrated on only one of these parameters, survivorship by killing plants, in order to minimize yield losses due to competition. Scant regard has been paid to the minimization of populations. Little is known about the relative importance of the basic mechanisms regulating the population dynamics, and suffice to say, even less attention has been assigned to determining the mechanisms critical to the strategic and efficient management of weed populations.

Using a generalized simulation model to explore the sensitivity of population growth to 'imaginary, one-at-a-time' regulation of transitional fluxes, Medd (1992) concluded that control of seed production resulted in slightly greater reductions in population growth than did the control of seedlings or a reduction in recruitment. In contrast, reducing seed persistence had minimal impact on population growth, whereas increasing recruitment led to significantly faster population growth. This was amplified by Pandey *et al.* (1993) who attempted to evaluate the returns from research into alternative avenues of weed management.

The predicted decline in populations arising from the control of seed production indicates that reproduction is a key to the persistence of wild oats in winter cropping. This contrasts with the commonly held premise that wild oats persistence is attributable to the accumulation of seed in the seed bank due to dormancy and seed longevity mechanisms (e.g. Adkins and Adkins 1994). The rapid decline in populations when seed inputs are reduced provides strong evidence that the mechanism of persistence is reproduction, **not** seed carry over or longevity. This is clearly evident from the prevention of seed production through clean winter fallowing which lead to dramatic reductions in the seed bank after only one year (Philpotts 1975, Wilson *et al*. 1977, Martin and Felton 1993). After two years the decline is about 99% (Philpotts 1975), which agrees closely with a seed bank half-life of six months estimated by Martin and Felton (1993). This suggests that wild oats are more likely to have transient seed banks (*sensu* Grime *et al.* 1988), with minimal carry over from year to year and therefore little accumulation of a persistent seed bank. Clearly, however, there is a small long lived component of the seed bank which is intractable (see e.g. Thurston 1966).

In considering the options indicated by Medd's simulation studies for reducing population growth, there are few practical ways of reducing seedling emergence in broadacre dryland cropping systems, apart from burying seeds by deep inversive ploughing. As summarized by Wilson and Peters (1992) and Nietschke (1996), shallow non-inversive tillage stimulates population growth of wild oats because seed is retained on the soil surface. Besides the prohibitive cost of ploughing and the current desire to minimize tillage, deep burial in itself is counterproductive. Burial prolongs the longevity of seed (Thurston 1961), most probably due to dormancy being enforced by the inoxic and moister storage environment (Simpson 1990). If brought to the surface by subsequent tillage, seeds are released from dormancy and become available for recruitment.

It has been argued that by understanding the processes regulating seed dormancy, chemicals capable of inducing prolonged dormancy might be discovered. Whilst a number of chemicals have utility in stimulating recruitment (Egley 1986, Taylorson 1987), few that reduce or prevent germination have been identified and none of practical value have eventuated.

Reducing plant survival is the predominant method of weed control. But concentrating on plant kill tactics is not the ultimate answer, particularly if the emphasis on herbicides continues to dominate other options. Striving for high levels of seedling mortality with herbicides intensifies the selection pressure, promoting herbicide resistance. Since modern herbicides generally have high efficacy, the marginal cost of achieving any improvement may be very high. Furthermore, considerable finesse would be required to implement such technology in order to overcome environmental variables. There is, however, considerable merit in augmenting the plant kill action of herbicides with other chemical, cultural or biological control options. The use of competitive crops and crop cultivars, and higher sowing densities, particularly warrant closer attention by farmers as tools that can be used at little cost to enhance the containment of wild oats. Is there a distinction between competition from competitive cultivars and higher crop density? The latter can be immediately invoked at minimal research cost.

A number of methods to directly attack seed production now seem practical, especially 'selective spray-topping' which gives a high level of control over seed set (Medd *et al.* 1992 and 1995, Nietschke and Medd 1996). The tactic employs avenacides during late tillering to early stem elongation—much later than is normally recommended for control of plants—and so has no benefits for preserving yield. To take advantage of this concept, further work is being undertaken by the author and colleagues with a view to registering flamprop-methyl for control of seed production. Negotiations with the primary registrant, Cyanamid, are at an advanced stage and it is likely the technique will be trialed on a broader scale in 1996.

Deployment of microbial pathogens has also been suggested as one prospective means of seed control (Medd and Campbell 1996, Hetherington and Auld 1996). Other avenues for regulating seed production could be to arrest seed formation by preventing fertilization or seed formation, but to these ends, there are no worthwhile prospective tools yet apparent. Because wild oats shatter, methods aimed at removing seeds with the harvest are unlikely to be useful, however, burning of stubble can destroy seeds in the litter (Nietschke 1996). A synergistic effect of burning and deep ploughing, was demonstrated in the United Kingdom (Wilson *et al.* 1984). However neither burning or deep ploughing is encouraged under conservation tillage ethics in Australia.

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Cultural weed management of wild oats

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Introduction

A range of cultural control techniques can be utilized for weed management in southern Australian cropping systems. These include; sanitation, cultivation, delayed seeding, increased crop competition, fertilizer use and placement, windrowing, weed seed collection at harvest, crop stubble burning, crop rotation, allelopathy, green manuring, hay making, silage, pasture slashing and livestock grazing. These strategies are reviewed as control methods for wild oats (*Avena* spp.).

Sanitation

Immigration of most wild oats into a field can be prevented by planting clean seed, cleaning harvest and tillage equipment between fields, and covering grain trucks used to transport grain (Thill *et al.* 1994). In the United Kingdom wild oats were found in 15% of cereal seed drills which were sampled at sowing (Elliott and Attwood 1970), whilst the transport of infested cereal straw bales has also been implicated as a source of wild oat seed spread (Wilson 1970).

Cultivation

Deeper burial of wild oat seed favours longer dormancy and thus increased longevity. If brought to the surface by subsequent tillage, seeds are released from dormancy and become available for recruitment (Medd in press). Consequently, wild oat populations tend to increase more under pre-sowing cultivations than practices which involve no or minimal soil disturbance such as direct drilling (Medd 1990, Walsh 1995). Wilson (1978) found that wild oat seed banks decline more rapidly using tyned compared with ploughing implements which inverted the seed.

Delayed seeding

Delaying the date of seeding allows increased wild oat seedling emergence before sowing, thus reducing weed infestation levels in the subsequent crop. Consequently, those fields with the worst wild oat populations are recommended to be planted last at seeding. Overseas research has shown that continuous late sowing can effectively control *A. fatua* L. populations (Whybrew 1964). Conversely, Walsh (1995) in Victoria determined that delayed seeding of wheat did not affect wild oat populations, due to the extended germination pattern of the weed. Furthermore, the practice usually results in lower grain yield and or quality and is therefore considered an uneconomic control method.

Crop competition

Competitive interactions between wild oats and crops are a very complex issue. Several agronomic factors will influence the extent to which crop yield is reduced by wild oats, and the amount of wild oat seed returned to the soil (Thill *et al.* 1994). Crops and crop cultivars differ in their competitive ability with wild oats. In Canada, barley is considered the most competitive grown crop species, followed by canola, wheat and linseed (O'Donovan and Sharma 1983). Increasing the seeding rates of cereal crops generally reduces wild oat competition (O'Donovan and Sharma 1983), whilst planting high quality crop seed at a relatively shallow depth gives the crop maximum competitive advantage in the early stages of growth (Cussans and Wilson 1976). Crops sown in narrow row spacings, are equal to or more competitive with wild oats than widely spaced crop plants (Thill *et al.* 1994).

Fertilizer use and placement

Of the many studies of interference between *A. fatua* and cereals, some have shown that nitrogenous fertilizers increase yield loss, some show a decrease and others show no effect (Cousens and Mortimer 1995). Recently, Walsh (1995) determined that the addition of fertilizer (nitrogen and phosphorus) to increase crop competition with wild oats, failed to achieve any reduction in growth and development of the weed. Nitrogen fertilizer can stimulate wild oat emergence before sowing, but as a long term means of reducing wild oat infestations, has little effect (Watkins 1971). Preliminary