CURRENT STATUS AND FUTURE TRENDS IN GRASS WEED OCCURRENCE AND CONTROL WORLDWIDE

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ABSTRACT

Contrasting the prevalence of grass weeds worldwide in 1977 with those today, there remains cause for concern. Grasses persist in all of the principal crops and evolution of herbicide resistance has occurred in many species. These conclusions emphasize the need for integrating weed management practices in the context of the ecology of target species. Knowledge relating to the persistence of grass weeds renewing both clonally and by seed is reviewed and further research directions are considered.

INTRODUCTION

Ten years ago (Terry, 1991) reflected that there is 'little cause for optimism that farmers in developing countries will cope any better with grassy weeds than those in the developed world where, despite the use of relatively advanced technology and high inputs, many grasses and sedges are still major weeds'. In the decade since that remark was made, the emergence of herbicide resistance in grasses on a substantial scale clearly indicates that many grass species successfully retain their status as important weeds. Over the same time period, there has been the commercialisation and increasing adoption of herbicide resistant crops for broad-spectrum weed control; farmers in the developing world have continued to face the similar weed problems (Akobundo, 1996); and there have been calls for an increasing awareness of the need to develop and implement integrated weed management practices (Jordan, 1992). This paper overviews some of the major grass weeds from an agro-ecological perspective and considers approaches and directions for research based on their biology and ecology for improved management.

GRASS WEEDS

Current taxonomic treatments of the grass family (Poaceae, Gramineae) recognise about 10,000 species and between 650 to 785 genera (Watson & Dallwitz, 1992). This family constitutes the fourth largest family in the Plantae and is agriculturally by far the most dominant and important (Heywood, 1978). However only a very small number (40–50) of species are serious weeds* and a judicious socio-economic perspective often has to be taken when considering the relative importance of many tropical species which have multiple farm uses, Maillet (1991). In their extensive compilation of weeds world-wide, Holm *et al.*, (1977) arranged 76 weed species into two groupings, the first having 18 which were quoted

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* It seems common practice in papers in this symposium series for authors to devote space to the definition of a weed, especially with the increasing interest on invasive species and genetically modified plants. I have resisted the temptation and refer the reader to an approach to definition given earlier (Cousens & Mortimer, 1995) and to previous symposia papers. Randall (1997) also provides a fullsome review of definitions.

Table 1. The major grass weed species according to Holm *et al*., 1977. Crops: Diverse indicates a wide range of seasonal crops, only main crops are indicated. Distribution: in some instances, limits are associated with warmer coastal areas.

Species	Center of origin	Distribution	Principal crops	Herbicide resistance
Cynodon dactylon	Tropical Africa	45 N - 45 S	Diverse : corn, cotton, sugar cane, vineyards and plantation crops	
Echinochloa crus-galli	Indo-European	50 N - 40 S	Diverse : corn, cotton, rice sugar beet	Synthetic auxins, dinitroanilines, triazines, chloroacetamides and others, thiocarbamates and others, triazines, ureas and amides
Echinochloa colona	India	45 N - 40S	Diverse : corn, rice, sorghum, sugar cane	Ureas and amides, ACC-ase inhibitors
Eleusine indica	India	45 N - 45 S	Diverse : corn, cotton, rice, sugar cane	ACC-ase inhibitors, bipyridiliums, dinitroanilines, glycines
Sorghum halepense	Mediterranean	55 N – 45 S	Diverse : corn, cotton, sugar cane, vineyards	ACCase inhibitors, dinitroanilines ALS inhibitors
Imperata cylindrica	Tropical Asia	45 N – 45 S	Diverse : plantation crops; those grown with slash and burn agriculture	
Digitaria sanguinalis	Tropical Asia	50 N – 40 S	Diverse : corn, cotton, peanut sugar cane	ACC-ase inhibitors, triazines
Avena fatua; *A. sterilis; A. ludoviciana*	Central Asia	World wide, where cereals grown	Diverse : small grain cereals, sugar beet	ACC-ase and ALS inhibitors, arylaminopropionic acids, dinitroanilines, pyrazoliums, thiocarbamates
Paspalum conjugatum	Tropical America	Humid tropics	Plantation crops	
Rottboellia cochinchinensis (syn *exaltata*)	Indo-European	23 N – 23 S	Diverse : corn, cotton, rice, sugarcane, soybean	ACC-ase inhibitors

as the world's worst weeds (Table 1). Twelve of these belonged to the family Poaceae, fourteen more grass genera being present in the second group. The choice of inclusion and of ranking was admittedly qualitative but based upon the best available knowledge of species ubiquity in cropping systems, world distribution and damage to crops in the considered opinion of the authors and their correspondents.

In 1977, triazine resistance in grasses had already been reported (Heap, 1997; 2001). Nearly a quarter of a century later, there are many grass species which are herbicide resistant (Table 2), most of which were not included by Holm and co-authors and three of which at least (*Echinochloa colona,* Valverde *et al.*, 2000; *Lolium rigidum*, Matthews, 1994; and *Phalaris minor*, Singh *et al.*, 1999) continue to have major economic and social consequences to farmers. Moreover, the evolutionary responses in two (*Lolium rigidum* and *Eleusine indica)* to glyphosate have been influential in the debate over the deployment of herbicide resistant grain crops, the likelihood and pattern of herbicide resistance evolution and implications for weed management (Powles & Shaner, 2001). A superficial answer to the title of this paper (borrowing from Partington, 1993) would be that 'grass weeds are alive and well and living in all cropped areas of the planet despite the attention of *Homo sapiens*.'

Whereas there is arguable justification for continuing to consider the species in Table 1 as major weeds, not all of these species listed in Table 2 fall in the same category. The evolution of resistance in a species may be a happenstance of broad-spectrum herbicide use against a primary target in a plant community and resistant biotypes of other species remain highly localized, range expansion being checked by other agencies. Moreover, there are grass species that have not evolved resistance that remain important weeds, for example *Anisantha* (syn *Bromus*) *sterilis* (Peters *et al.*, 1993), *Aegilops cyclindrica*, *Bromus tectorum*, *Secale* spp (Anderson, 1998) and *Panicum miliaceum* (Cavers & Bough, 1985).

YIELD LOSSES DUE TO GRASS WEEDS

Bunce & Ziska (2000) considered that production losses due to weeds under best management practices in the US where herbicide use is widespread was about 7% of attainable yield, averaged over nine principal crops (barley, maize, cotton, potato, paddy rice, sorghum, soybean, sugarcane and wheat). In the absence of herbicide use, losses averaged 35%. For each crop, Bridges (1992) concluded that at least one grass weed species was inadequately controlled and interfered with crop yield, crop quality or harvest efficiency, in many but not all cases having been recorded earlier by Holm *et al.*, (1977).

However, ranking the comparative damage to production done by individual weed grass species is fraught with difficulty given the interaction of factors that initiate the onset of competition between plant species, the dynamics of differential resource acquisition that occurs during weed-crop interference and damage in addition to strict yield loss. In comparing the tolerance of *Triticum aestivum* cultivars to *Lolium rigidum,* Cousens & Mokhtari (1998) reported little correlation between competitiveness across seasons within a single location or locations across seasons. Yield losses from this weed at densities from 200-500 plants/m^{-2} ranged from 0–100% (Lemerle *et al.* 1995). Similarly large intersite variation has been recorded for competitiveness of *Aegilops cyclindrica* in wheat in the US (Jasieniuk *et al.*, 2001).

Table 2. Grass weeds (bold) in Group 2 from Holm *et al.*, 1977 and those that have evolved herbicide resistance subsequently (Heap, 2001). Original taxonomic nomenclature has been retained.

Species	Herbicide
Agropyron repens	
Agrostis stolonifera	Triazoles, ureas, isoxazolidiones
Alopecurus japonicus	Ureas and amides
Alopecurus myosuroides	ACC-ase and ALS inhibitors, dinitroanilines, ureas and amides
Brachiaria mutica	
Brachiaria plantaginea	ACC-ase inhibitors
Bromus diandrus	ACC-ase inhibitors
Bromus tectorum	ALS inhibitors, triazines, ureas and amides
Chloris inflata	Triazines, ureas and amides
Dactyloctenium aegyptium	
Digitaria scalarum	
Digitaria ischaemum	ACC-ase inhibitors
Echinochloa crus-parvonis	Synthetic auxins
Echinochloa phyllopogon	ACC-ase inhibitors, thiocarbamates
Eleusine indica	ACC-ase inhibitors, bipyridiliums, dinitroanilines, glycines
Hordeum glaucum	ACC-ase inhibitors, bipyridiliums
Ischaemum rugosum	Bipyridiliums
Leersia hexandra	
Leptochloa panicea; L. chinensis	
Lolium temulentum	
Lolium multiflorum	ALS and ACC-ase inhibitors, ureas and amides
Lolium perenne	ALS and ACC-ase inhibitors
Lolium persicum	ACC-ase
Lolium rigidum	ALS and ACC-ase inhibitors, chloroacetamides, dinitroanilines, isoxazolidiones, glycines, mitosis inhibitors, thiocarbamates triazoles, ureas and amides
Panicum maximum; P. repens	
P. capillare; P. dichotomiflorum	Triazines
Paspalum dilatatum	
Pennisetum clandestinium; P. polystachyon; P. pedicellatum; P. purpureum	
Phalaris minor	ACC-ase inhibitors, ureas and amides
Phalaris paradoxa	ACC-ase inhibitors, triazines
Phragmites australis; P. karka	
Poa annua	Triazines, traiazoles, ureas isoxazolidiones, bipyridiliums, thiocarbamates, ureas and amides, dinitoanilines
Setaria verticillata; S. viridis;	ACC-ase and ALS inhibitors dinitroanilines and triazines
S. faberi; S. glauca; S. lutescens	
Sorghum sudanense	ACC-ase inhibitors
Urochloa panicoides	Triazines
Vulpia bromoides	Bipyridiliums

Whilst recognising this inherent difficulty, Swanton *et al.*, 1999 reviewed both reported and extrapolated threshold densities (single season economic thresholds, *sensu* Cousens, 1987) and concluded that annual grasses were less competitive that broad leaved weeds in corn and soybean in N. America. Contrastingly, Gerowitt & Heitefuss (1990), for European cereals (wheat and barley), argued that thresholds were lower for grass weeds than for broad-leaved species.

The *Echinochloa* species have long been recognised as serious weeds in many temperate and tropical crops (Barrett, 1983, Norris 1992), and rice yield losses span a similarly wide range to those in wheat due to *L. rigidum*, depending on crop establishment method and agronomic practice (Kropff & van Laar, 1993). *E. phyllogon* and *E. oryzoides* constitute the principal grass weed threats to direct seeded rice in California. With the exception of this state, red rice (an ecotype of *Oryza sativa*) is an additional damaging rice weed in the US (Gealy *et al.*, 2000) as well as in S. America (Fischer and Antigua, 1996) as are wild rices (*O. longistaminata* and *O. barthii*) in Africa. In south-east Asia, the recent emergence of phenotypically diverse populations of 'weedy rices' (Cohen *et al.* 1999) provides a further example that threatens direct seeded rice, especially in Malaysia and Vietnam.

Whilst *Avena* and *Phalaris* species are serious grass weeds in many Mediterranean countries, India and N. America, *Avena* species are reported as economically more damaging than other grass weeds in Australia, Europe and N. America, (Martin & Field, 1987; Wilson & Wright, 1990; Carlson & Hill, 1985). *Setaria* species are however widespread throughout maize and soybean production areas in N. America. In the rice-wheat systems of the Indo-gangetic plains, *Phalaris minor* is now considered to be the predominant grass weed (Singh *et al.* 1999). In Costa Rica and elsewhere in Mesoamerica, *Rotboellia cochinchinensis* is considered by farmers as a very serious weed of maize in particular but also causes significant yield losses in upland and rainfed rice (Valverde *et al.* 1999). *Alopecurus myosuroides* (Clarke & Moss, 1991) and *Bromus sterilis* (Cussans *et al.* 1994) continue to occur as major cereal weeds in the UK under reduced tillage.

Of the tropical species identified by Holm *et al.*, (1977), that exhibit clonal growth, *Cynodon dactylon*, *Imperata cyclindrica*, *Paspalum* species and *Sorghum halepense* continue to retain their status as major weeds world-wide. *C. dactylon* constitutes a major weed of grassland, grain and young plantation crops, displays a wide global distributional range, its growth being limited by low temperatures in temperate regions. It poses a threat in minimally tilled grain crops (Broome *et al.*, 2000) and particularly in developing countries where reliance is placed on manual methods of weed control (Akobundo, 1996).

Garrity *et al.*, (1997) estimated that there were 35 million ha of *Imperata* grassland in Asia. Land denudation by slash-and-burn agriculture, logging and burning provides an early successional habitat in which *I. cylindrica* can expand, the weed being an aggressive grain crop competitor (Brook, 1989) as well as being damaging to young plantation crops (Conroy & Bagnall-Oakley, 1995). The species is widespread in Africa (Chiyoke *et al.*, 2000; Akobundo & Ekelme, 2000), an invasive weed elsewhere (e.g. USA, King & Grace, 2000) and locally problematic in perhaps one of the world's most labor intensive weed management systems, upland slash and burn agriculture in Lao PDR (Roder, 2001). Relatively less attention appears to have been placed on quantifying the damage done by *Paspalum* species but over-exploitation of grasslands in Central America and in the Caribbean renders pastures open to invasion by *P. virgatum*, substantially reducing their commercial value (de La Cruz *et al.*, 1994).

IMPROVING GRASS WEED MANAGEMENT

The foregoing discussion clearly indicates that grass weeds will continue to hold center-stage in demanding attention in the immediate future. The fact that crop yield losses may be substantial but highly variable, in those species that have been closely examined, and the emergence of herbicide resistance point to this conclusion.

Whilst worldwide improvement of grass weeds management will undoubtedly be achieved with the further diffusion and adoption of existing technologies, together with the discovery and registration of new graminicides especially with new modes of action, sustainable improvement will come in the context of resistance management and integrated weed management practices. Yet Owen (2000) and Pannell & Zilberman (2000) argued that the adoption of integrated weed management practices to delay and to manage herbicide resistance will be driven by a complex of socio-economic considerations, in addition to the demonstration of technological alternatives. Major factors are profitability when anticipating the cost of herbicide resistance in the long term and the options for change in relation to adjustment costs. Whether the intention in the design of integrated weed management systems is proactive to the anticipated loss of a control option or reactive to it, knowledge of ecological and evolutionary responses in weed species are essential in designing and assessing innovations before submitting them to the forge of farmer adoption. This is undoubtedly true for grass weeds that, to varying extent, mimic cereal crops in life history, and often constitute the major weed. It is thus pertinent to examine the processes that govern both the persistence of grass weeds in the face of weed control and their spread and distribution. The global impact of grass weeds is intimately inter-related to a) the ecological amplitude of species and b) resilience to control measures.

Ecological amplitude

Ecological amplitude has often been couched in terms of innate physiological tolerance of a genotype but the ability of a species to invade and persist in differing habitats depends also upon the amount and organization of genetic variation within and between populations (Ennos, 1997). Moreover habitats may not only be characterized agro-climatically but also in the context of the pattern of induced disturbance regimes of cropping practices themselves. Hence traits conferring ecological amplitude may be seen at various levels (physiological to life history) both within and amongst populations.

In the Poaceae, diversity both in life form (semi-determinate to indeterminate in a modular construction, Harper *et al.*, 1986) and of life cycles (semelparity/iteroparity, Begon *et al.*, 1990) is also conspicuously evident in patterns of tillering, flowering and of clonal growth, with inherent life history compromises (Law *et al.* 1977). Precocity in reproduction ('ephemerals', e.g. *Poa annua*), seasonal semelparity (short-lived 'annuals' e.g. *Bromus sterilis*) and iteroparity (long-lived 'perennials', e.g. *Imperata cyclindrica*) are arguably life histories that are optimal for arable habitats that present periodicity in intensity and regularity of disturbance. Temporal environmental variability over generations introduced for example by crop rotations, timing of crop sowing and harvesting, timing and frequency of ploughing and land preparation, favors adaptations that mitigate against detrimental demographic events and the role of seed dormancy as a 'bet-hedging' trait is well known (Kalisz *et al.* 1997 and references therein). Within grass species, ecotypic differentiation in a wide range of traits and life history variation is commonly reported in the literature (Bazzaz, 1996). Ecological amplitude at the species level is well illustrated in the range expansion of *Bromus tectorum* in the Great Basin rangelands in North America (Mack, 1981). From a comparative study in the same site, this species was found to behave simultaneously as an ephemeral monocarpic, annual monocarpic or winter annual monocarpic species. The ability to display multiple fecundity schedules precludes its extinction in a range of disturbance regimes (often fire mediated).

The ranges of latitude of species in Table 1 attests not only to the distribution of agro-ecosystems of particular crops but the climatic range of weeds. Physiological tolerance to climate in a grass is exemplified by the invasion of the subantarctic island of South Georgia by *Poa annua* (Leader-Williams, 1987). *Echinochloa crus-galli*, although possessing a C_4 photosynthetic pathway, has evolved cold temperature adaptations (Potvin & Simon, 1989) and is native to Europe, South and S.E. Asia (Maun & Barrett, 1986), has established in cold temperature zones in North America (Robert *et al.*, 1983*)* and probably now occurs in West Africa (Danquah, Karp, Johnson and Riches, pers comm). In the last 15 – 30 years, *Sorgum halepense* another C_4 species has shown poleward range expansion in N. America (Warwick, 1990) and is also now reported in Switzerland (Schmitt, 1995).

Resilience to control

At the field level, resilience to control is an expression of the net fitness of a plant species in an agroecosystem, of which fecundity (asexual and sexual), mortality and dispersal are integral components. Answers to why an individual species continues to renew populations in crops under weed management ultimately comes from an analysis of the population dynamics of a species and understanding the relative sensitivity to control throughout stages of the life-cycle. In considering why a species has become invasive or persists in an agro-ecosystem, many authors (e.g. Perrins *et al.*, 1992, Williamson, 1996) have suggested that a more successful approach derives from a comparision of the characters that differ between pairs of closely related species, one of which is a weed and one is not; and of the merits of multi-site/habitat comparisons of individual weed species responses (Cousens & Mortimer, 1995; Freckleton & Watkinson, 1998). In the absence of such research, the best that can be drawn from the often copious literature on grasses are limited inferences based on autecological observation.

Resilience and clonal growth

Clonal growth in grasses is an obvious example of a growth strategy that may confer resilience. The capability of producing long horizontal shoot axes (stolons, rhizomes etc) not only offers escape from competitive pressure from neighbours by increased lateral growth but also presents a bank of above/below ground meristems from which regrowth of aerial shoots may occur. Asexual reproduction (*sensu* Silander, 1985) may arise by modular fragmentation given that meristematic totipotency is present at nodes, whether modules be tillers, stolons or rhizomes.

Tropical grasses such as *Imperata cyclindrica* and *Sorghum hal*epense are renown for their rate of rhizome production and for the potential buildup of underground biomass (8.9 t ha of *I. cylindrica* rhizomes has been recorded in abandoned tropical fields, Akobundo & Ekeleme, 2000). However the relative contribution to population growth rates of sexual reproduction (seeds) as opposed to clonal ramets has rarely been examined quantitatively for most grass weeds. In *I. cyclindrica* management, land clearance by burning or pulling promotes bud break and rapid regeneration from rhizomes (Eussen, 1981) and is probably the principal reason for its persistence in shifting agriculture. Seed production in this species is prolific yet Brook (1989) concluded that turnover in seed banks of *I. cyclindrica* may be relatively high since the longevity of seeds is approximately 12 months and seedling recruitment may be relatively low. In *Elymus repens* in winter wheat in the UK, elasticity analysis (Mortimer, 1984; Silvertown *et al.*, 1993) indicated that clonal growth from buds on rhizomes at the field level was a much greater contributor to overall population growth rate than seeds when land was both ploughed or minimum tillage with glyphosate was practiced. Conversely in *S. halepense*, seed longevity in the soil may extend up to 6 years (Leguizamón, 1986) and the fact that *S. halepense* has shown substantive range expansion in the US, mostly in monocultures of soybeans and maize (Warwick 1990) points to the importance of seed in founding populations. *S. halepense* is also considered a noxious seed contaminant in grain imports to China (Yan & Yin, 1994).

Nevertheless, the dynamics of meristem banks in grass weeds remains poorly understood and researched given the importance of herbicide translocation in stolons and rhizomes in most grass weeds. From experimental comparisons of *Agrostis stolonifera* (stoloniferous), *Holcus mollis* (rhizomatous) and *C. dactylon* (stoloniferous and rhizomatous), Dong and Pierdominici (1995) suggested that stolons serve primarily as foraging organs for light, whereas the main function of rhizomes was presentation of meristems and storage of carbohydrates, irrespective of whether the grass species involved produced both rhizomes and stolons. In *C. dactylon*, biomass allocation to stolons was less variable than allocation to rhizomes in response to light and nutrient treatments (Dong & De Kroon, 1994) supporting this contention. Both cultivation leading to vegetative fragmentation and removal of above ground shoots, either manually or with non-translocated herbicides, serves to release meristems from dormancy and to commit nutrient and energy reserves stored in rhizomes to shoot and root growth. Depending on the depth of burial, these may lead to fragment death through dessication, failure of shoots to emerge above the soil surface, and variation in shoot vigor of emerging plants. Whilst *C. dactylon* rhizome segments are sensitive to dessication on the soil surface, they may readily emerge from depths as deep as 30 cm (Maillet, 1991). Similarly those of *I. cylindrica* may emerge from 15 cm (Brook 1989). Eussen (1981) and Wilcut *et al.*, (1988) have noted variability in the occurrence of axillary nodes in *I. cylindrica* and suggested that the number of buds towards the apex of the rhizome is more important than rhizome biomass in regeneration. Both internal and external regulation of bud-break and shoot emergence is well known to be complex and to be governed at least by thermal time, light quality and the size and age of rhizomes and stolons (Ghersa *et al.*, 2000).

Success then in maximizing control of these clonal grasses results from an understanding of the phenology of sprouting, the exhaustion of reserves and methods of prohibition of subsequent rhizome development. This is well advanced in *S. halepense*. Satorré *et al.*, (1985) identified seasonal changes in the below ground biomass of *S. halepense* and, based on predictions of rhizome biomass allocation and bud dynamics, Benech-Arnold *et al.*, (1989) advocated changes to a) cropping patterns to maximize the efficacy of weed suppression by the crop and b) the targeting of time of herbicide application to periods when plants had the least available reserves. These changes significantly reduced the population growth rate of the weed (Vitta & Leguizamon, 1991; Van Esso & Ghersa, 1993).

Resilience and reproduction by seed

In contrast to clonal species, considerable more progress has been made in understanding the resilience of grasses that reproduce by seed. Empirical modelling approaches have been explored in detail to explore the relationships amongst demographic factors that regulate weed populations (Mortimer *et al.*, 1989; Cousens & Mortimer,1995; Kropff *et al.*, 1996), their integration with economic decision making (Pandey & Medd, 1991; Jones & Medd, 2000) and long term approaches to weed population management (Wallinga & Van Oijen, 1997, Wallinga, 1998). Past emphasis has been placed upon the use of tillage practices and graminicides to reduce yield losses. It is only relatively recently that approaches based upon management of seed banks have been more closely considered.

Where seed banks are transient (< 1 year) tillage practices have a dominant influence in determining species persistence. Comparative studies of *Bromus* species illustrate this well. *Bromus sterilis* is a strong competitor of winter wheat in the UK (Cousens *et al.*, 1988) under reduced tillage and can rapidly achieve high infestations. Lintell Smith *et al.*, (1999) concluded that the species had a finite rate of increase of ca 130 fold in the absence of intraspecific competition and that per capita growth rates were strongly driven by density dependent recruitment of seedlings and seed output of mature plants. Such features provided the ability to strongly buffer population densities against seasonal variations and seed losses before seed bed preparation, in the absence of in-crop weed control. However as has been concluded elsewhere (Peters *et al.*, 1993), persistence is related to the depth of seed bed cultivation which is critical in determining seedling recruitment.

Table 3 illustrates this by comparative analysis (Howard, 1991) of three species related to *B. sterilis*. By the mid-1980s, *B. sterilis* had become noted as an important grass weed in reduced tillage systems (Froud-Williams & Chancellor, 1982) and subsequently *B. commutatus* was reported to be increasing in abundance in the UK (Cussans *et al.*, 1994). *B. interruptus* on the other hand was considered extinct in the UK in the 1970's (Lucas & Synge, 1978). Persistent seedbanks for all species are not reported although limited induced dormancy (Peters *et al.*, 2000) may occur. All species survived to set seed if established at the same time as a winter wheat crop in the UK (Mortimer *et al.*, 1993). *B. sterilis* typically initiated seed dispersal earlier than the other species, with the consequence that some seed were shed before crop harvest. Conversely, relatively less seeds of this species were present in the panicle at harvest time. Combine harvesting acted differentially in that some species *(B. interruptus and B. commutatus)* were more likely to be dispersed with the chaff and others *(B. sterilis,* in particular) retained with the grain (Howard *et al.,* 1991). Taking into account these factors (time of initial dissemination, rate of dissemination, and losses due to combining), the greatest proportion of seeds present on the ground after crop harvest was for *B. interruptus* and *B. mollis* and least for *B. commutatus* (Table 3). The chance of these seeds then surviving fallow conditions and initial seedbed preparation is controlled by dormancy patterns in August and September. The absence of dormancy mechanisms (after-ripening and photo-induction) in *B. interruptus* characteristically resulted in precocious germination with

Table 3. A comparative analysis of four brome grasses in UK winter wheat in the absence of grass weed control. [1] Takes into account dissemination rate and losses due to combine harvesting. [2] These data subtracted from unity give the cumulative proportional mortality post-dispersal and up to and including losses in initial land cultivation in seedbed preparation. [3] Based on pot experimentation. No losses are assumed between seedling emergence and harvest. Data taken from Howard, 1991, and Mortimer *et al.*, 1993.

Species	Probability						Mean seed production per plant in wheat	Net reproductive rate by depth	
	Seed dispersal to the ground by crop harvest [1]	Seed survival prior to crop sowing [2]	Seedling establishment from a depth of [3]		Plant survival to reproduce at harvest by depth				
			50 mm	100 mm	50 mm	100 mm		50 mm	100 mm
B. commutatus	0.66	0.20	0.60	0.02	0.079	0.0026	585	46.2	0.4
B. interruptus	0.87	0.005	1.00	0.00	0.004	0.0	416	1.7	0.0
B. mollis	0.81	0.45	0.14	0.03	0.051	0.0109	422	21.5	4.6
B. sterilis	0.77	0.40	0.50	0.04	0.154	0.0123	479	73.8	5.9

late summer rains and the consequent death of seedlings in initial seedbed preparation for the coming crop. Losses were experienced by the other three species, but to a lesser degree. However the depth at which seeds are placed through cultivation in seed bed preparation was a critical factor in determining the likelihood of seedling establishment in the crop. Howard (1991) found that *B. interruptus* was unable to establish seedling populations after relatively deep burial in the soil (10 cm) and the successful fraction of other species was low. At shallow (reduced-cultivation) depths, *B. interruptus* readily established, as did *B. commutatus* and *B. sterilis* but to a lesser extent. *B. mollis* was the least likely to establish seedling populations. Net reproductive rates (the product of survivorship to harvest and mean seed production per plant) enables a ranking of the relative performance of each species from which it is clear that the combination of practices that determine post-harvest seed losses and seedling recruitment according to depth of cultivation have a selective and major influence on reproductive rate (Table 3) and hence persistence.

In contrast to the brome grasses, *Avena* species exhibit seed longevity and persistent soil seed banks occur in *A. fatua, A. sterilis* and *A. ludoviciana*. Seed dormancy and germination behaviour is highly variable amongst species and populations and over 50% of buried seed may be lost each season. Successful long term management not only relies in minimising recruitment of seedling cohorts into the crop and prohibiting seed return to ensure the decline of these seed banks. From the available literature, population growth rates would in general appear to be much lower than those estimated for *Bromus sterilis* (e.g. Gonzalez-Andujar & Fernandez-Quintanilla, 1991). Martin & Felton (1993) concluded that as little as 3-6 % recruitment of reproductive plants from the seed bank maintained populations and continuous wheat rotations in Australia using herbicides were much less effective in reducing the weed seed bank than one incorporating a sorghum crop and a winter fallow. Similar conclusions were reached by Gonzalez-Andujar & Fernandez-Quintanilla (1991) concerning use of fallows. Recently Jones & Medd (2000) argued that the integration of control tactics using dynamic optimal decision rules with a long term planning horizon not only maximized farm returns and but most rapidly exhausted the seed bank and for *A. fatua* was superior to the use of economic optimum thresholds (c.f. Doyle *et al.*, 1986 for *Alopecurus myosuroides*). The importance of these studies is that they provide a framework for assessing the merits of control tactics such as seed kill by spray topping with selective herbicides (Medd *et al.* 1992) or by seed collection and burning (e.g herbicide resistant *Lolium rigidum,* Gill & Holmes, 1997) and of more flexible herbicide policies that may delay the emergence of herbicide resistance (Pannell, 1995). The further fusing of this approach with those examining the population genetics of herbicide resistance (e.g. Diggle & Neve, 2000) will be a valuable next step.

Opportunities for enhancing grass weed control by focusing on post-harvest, fallow management practices and during land preparation prior to crop sowing hinges on an understanding of the environmental control of dormancy and germination (Benech-Arnold *et al.*, 2000). It is in this area that there remain major researchable issues for grass weeds. The value of the approach is well illustrated by the use of thermal time models with *Setaria* species to optimize dates for seedbed preparation (Forcella *et al.*, 1993) and for forewarning managers of the likelihood of weed emergence in relation to climatic events that may induce dormancy.

The extension of the approach to encompass hydro-thermal time represents a sophistication that will be important in improving decision making in relation to soil moisture and anaerobic soil conditions, especially in rainfed and direct seeded rice, where the water profile (flooding depth, duration and frequency) is known to be important in determining grass seedling establishment and growth (Hill *et al.*, 2001). Earlier sowing of wheat in rice-wheat rotations in India has been proposed as a tactic to suppress *Phalaris minor,* exploiting optimal low-temperature germination characteristics of this species. A constraint to adoption of this in the past has been the late maturation of transplanted rice and insufficient time for wheat field preparation. Direct seeding of shorter duration rice coupled with zero tillage of wheat, however enables a valuable cultural method for the control of *P. minor* coupled with other system benefits (Hobbs *et al.* 2001).

Evolutionary responses

Jordan & Jannink (1996) pointed out that whilst knowledge of evolutionary processes underlying herbicide resistance is increasingly underpinning management strategies (see Gressel, 2000), much less is known about rates of genetic adaptation to other weed management practices, the likely impact and the need to design systems that deliberately delay evolutionary shifts. Distinctive variation in life history and growth form is common in grass weeds and mechanisms maintaining genetic polymorphisms are various (Barrett, 1982; Jain, 1983). Past attempts to correlate a species' ecological amplitude and its overall genetic variability have met with mixed success (Huenneke, 1991) and Hamrick (1983) concluded that there was only weak correlation between geographical range and inter-population variation. However karyotypic differentiation in respect to climatic regions is present in *Cynodon dactylon* in Sri Lanka (De Silva & Snaydon, 1995). Populations from rice fields were found to contain both tetraploid and diploid plants whilst those from roadsides and lawns in the wet region and from forests in the hill country comprised only diploid individuals. Much earlier work with *Avena barbata* has also demonstrated population differentiation with respect to drought, Allard et al. (1978).

What is also clear is that in some clonal and predominantly inbreeding annual grasses at least, considerable genetic variability may be maintained within populations. For instance Cheng & Chou (1997) recorded molecular and morphological differentiation amongst and within populations of *Imperata cylindrica* in Taiwan and Sriyani *et al.*, (1996) have reported biotypic variability in response to glyphosate translocation within rhizomes. Whilst glyposate (0.5 – 1.0 kg ha^{-1}) was translocated throughout rhizomes in equal amounts by biomass, the extent and location of rhizome bud death and sprouting was biotype specific; interactions of the herbicide with mechanisms determining apical dominance being postulated as the cause. Microsatellite analysis of *Bromus sterilis* (Green *et al.*, 2001), which is predominantly inbreeding, indicated the existence of genetic diversity present as many separate and genetically distinct lines and both spatial localization and mixing of genotypes at the field level. Similar results were found using allozyme markers in *Avena* species by Allard and co-workers (Hamrick & Allard, 1972; Allard, 1977; Yazdi-Samada *et al.*, 1978) although not by Warwick (1990) for other species. The co-existence within populations of selfing lines that have diverged at many loci suggests that these selfing lines may have also retain heritable trait variation. Such findings are of obvious importance in considering the potential response to changes in weed management practices but also have implications for gene flow from transgenic grain crops. The maintenance of a genetic diverse weed population as a pollen recipient may result in more rapid spread of transgenes to closely related feral and weedy species such as rice, and be reflected in variation in performance of hybrids and backcross progeny (Snyder *et al.*, 2000; Arriola & Ellstrand, 1996).

CONCLUDING REMARKS

Returning to the opening remark, and having perused more literature than is reflected below, I am left with the conclusion that Terry's (1991) concerns remain. On the one hand, research into grass weed management must remain high on the agenda, and on the other, the direction is clearly indicated. At the heart of the approach is the paradigm shift towards weed management in which preventative systems are considered first and precision control is achieved when implementing necessary in-crop weed control. This theme is not new and has been strongly advocated in recent reviews on the future directions for weed science by leading weed science societies (for instance Hall *et al.*, 2000; Kropff & Walter, 2000).

Utilising preventative measures places a premium on understanding the ecology of individual weed species in the context of cropping systems, and agronomic practices, in which weed suppression through crop competition is of major importance. Successful management of *I. cyclindrica* has been achieved by exploiting the species sensitivity to shade. This however is predicated on ensuring soil fertility for cropping systems that enable abandonment of shifting agriculture and sustainable yield returns. These systems typically involve fallow management including life stock management, shrub legumes and short term timber cropping (Menz, 2000). In tropical grass weed control, the impact of preventative measures has also been clearly illustrated in the improved management of *Rottboellia cochinchinensis* through the integrated use of inter-sowing of legume crops, reduced tillage and pre-emergence herbicides, that have in combination led to soil seed bank decline (Valverde *et al.*, 1999).

Within the context of preventative measures, there is a compelling case for germplasm improvement for grass weed suppression as has been argued for *Lolium rigidum* (Lemerle *et al.*, 2001) and empirical screening methods of cultivars and inter-specific hybrids have been shown to be successful in rice (Johnson *et al.*, 1998). However understanding the dynamics of weed–crop competition in terms of traits that determine competitive ability and weed suppression remains a substantially undertaking. It is likely that currently available weed-crop simulation models (Bastians *et al*, 1997; Caton *et al.* 1999) will need to further take into account early seedling vigor (Asch *et al.*, 1999) shoot/root partitioning in competition for nutrients (Lindquist, 2001) as well the dynamics of weed and crop shoot morphology (Caton *et al.*, 2001). Moreover as Lemerle *et al.*, (2001) remarked, the extent to which deployment of competitive cultivars will select for evolutionary responses in weeds should be borne in mind. In genetically diverse grass weeds, co-adaptation may happen over relatively few generations (Allard, 1997). It maybe in this feature in particular, that grass weeds perhaps represent the greatest challenge in the design of integrated weed management practices.

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