

Breeding Cereal Crops for Enhanced Weed Suppression: Optimizing Allelopathy and Competitive Ability

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Abstract Interest in breeding grain crops with improved weed suppressive ability is growing in response to the evolution and rapid expansion of herbicide resistant populations in major weeds of economic importance, environmental concerns, and the unmet needs of organic producers and smallholder farmers without access to herbicides. This review is focused on plant breeding for weed suppression; specifically, field and laboratory screening protocols, genetic studies, and breeding efforts that have been undertaken to improve allelopathy and competition in rice, wheat, and barley. The combined effects of allelopathy and competition determine the weed suppressive potential of a given cultivar, and research groups worldwide have been working to improve both traits simultaneously to achieve maximum gains in weed suppression. Both allelopathy and competitive ability are complex, quantitatively inherited traits that are heavily influenced by environmental factors. Thus, good experimental design and sound breeding procedures are essential to achieve genetic gains. Weed suppressive rice cultivars are now commercially available in the U.S. and China that have resulted from three decades of research. Furthermore, a strong foundation has been laid during the past 10 years for the breeding of weed suppressive wheat and barley cultivars.

Keywords Plant breeding · Heritability · Allelopathy · Competition · Interference · Weed · Herbicide · Organic agriculture · Rice · Wheat · Barley

Introduction

Plant breeders around the world devote significant time and resources to breeding for improved yield, adaptation, and resistance against pests and diseases; but herbicide use is routine in breeding trials, essentially precluding selection for weed suppressive ability. In fact, research has suggested that historical cultivars often have better weed suppressive ability than modern cultivars (Lemerle et al., 2001a; Bertholdsson, 2004; Vandeleur and Gill, 2004; Wicks et al., 2004; Mason et al., 2007; Murphy et al., 2008; Wolfe et al., 2008). Interest in breeding grain crops with improved weed suppression is growing in response to the evolution and rapid expansion of herbicide resistant weed populations (Carey et al., 1995; Heap, 2012), and the unmet needs of organic producers (Wolfe et al., 2008; Hoad et al., 2012) and smallholder farmers in the developing world without access to herbicides (Courtois and Olofsdotter, 1998; Toure et al., 2011). In such smallholder systems, weeds are the major constraint to upland rice (*Oryza sativa*) production, and hand weeding is the major source of control (Johnson et al., 1998; Fofana and Rauber, 2000; Toure et al., 2011). Breeding for disease and pest resistance has led to decreased demand for fungicides and insecticides; however, herbicide use is still increasing in Asia and many other areas (Olofsdotter et al., 2002; Chauhan, 2012). Additionally, researchers have reported that yield losses due to weeds, particularly barnyardgrass (*Echinochloa crus-galli*), are increasing as Asian farmers switch from labor-intensive hand transplanting to direct seeded systems for rice production (Kim and Shin, 1998; Kong et al., 2011; Chauhan, 2012).

Weeds can be combated with cultural practices such as mechanical cultivation (Murphy et al., 2008), high density planting (Korres and Froud-Williams, 2002; Paynter and Hills, 2009; Beres et al., 2010), narrow row spacing (Champion et al., 1998; Drews et al., 2009), flaming (Knezevic, 2011), robotic

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weeding (van der Weide et al., 2008), cover cropping (Reberg-Horton et al., 2012), and the use of no-till residues (Nord et al., 2011). Developing grain cultivars with superior competitive ability against weeds will complement cultural methods for weed control in maintaining acceptable yields and suppressing weed populations. These crop plants likely will not eradicate weeds as thoroughly as synthetic herbicides, but rather allow for coexistence of competing weed plants with much reduced vigor (Fitter, 2003). Weed suppressive cultivars could be employed as a supplement to herbicides because herbicide performance is often improved when competitive cultivars are used (Lemerle et al., 1996). Less frequent or reduced rates of herbicide application in combination with competitive cultivars has the potential to be an economically viable alternative to conventional weed management (Gealy et al., 2003), although extended use of sub optimal herbicide rates is thought to hasten the development of herbicide-resistant weed populations.

Variation in weed suppressive ability has been observed between crop species (Satorre and Snaydon, 1992; Lemerle et al., 1995; Seavers and Wright, 1999; Bertholdsson, 2005) and among cultivars of the same species. An ideal crop cultivar will suppress weed growth and reproduction while maintaining acceptable yields in weedy conditions. The ability to sustain higher yields relative to other cultivars in the presence of weeds is sometimes referred to as tolerance (Goldberg, 1990). Many studies have found that weed biomass suppression and yield tolerance are broadly correlated (Challaiah et al., 1986; Wicks et al., 1986; Balyan et al., 1991; Huel and Hucl, 1996; Lemerle et al., 1996, 2001a; Fofana and Rauber, 2000; Gealy and Moldenhauer, 2012). Still others have found no relationship between tolerance and weed suppressive ability (Cousens and Mokhtari, 1998; Coleman et al., 2001). Jordan (1993) contended that tolerance and weed suppression can result from different mechanisms and may or may not be correlated. Therefore, these factors should be measured independently.

The weed suppressive ability of a given cultivar also can be described as its ‘interference potential’. Interference, the induced effect by an individual on a neighbor through changes in the environment, consists of the combined effects of competition and allelopathy (Harper, 1977). Competition is based on the ability of a crop cultivar to access scarce light, nutrients, and water resources in a limited space, thus suppressing the growth and reproduction of nearby weed species. Allelopathy is a process by which plants suppress neighbors by exuding phytotoxins into the near environment (Muller, 1969). The combined effects of allelopathic activity and the set of traits impacting competitive ability determine the interference potential of each cultivar. Allelopathy works in conjunction with competition, and breeders should strive to improve both simultaneously to achieve maximum weed suppression (Olofsdotter et al., 2002).

During the past 50 years many research programs have screened grain species for allelopathy and competition.

Allelopathy screenings have been conducted in a number of species including oat, *Avena sativa* (Fay and Duke, 1977); rye, *Secale cereale* (Perez and Ormenonunez, 1993; Reberg-Horton et al., 2005; Kruidhof et al., 2009; Brooks et al., 2012; Shulz et al., 2013); cassava, *Manihot esculenta* (Huang et al., 2010); sunflower, *Helianthus annuus* (Wilson and Rice, 1968); and sorghum, *Sorghum bicolor* (Alsaadawi et al., 1986; Cheema et al., 2009; Weston et al., 2013). Research on competitive ability has been conducted in several species including maize, *Zea mays* (So et al., 2009; Silva et al., 2010); soybean, *Glycine max* (Jannink et al., 2000; Place et al., 2011); sorghum (Guneyli et al., 1969; Wu et al., 2010); and canola, *Brassica napus* (Lemerle et al., 2010). In this review, we focus on examples from research and breeding efforts in rice (see also Kato-Noguchi and Peters, 2013), wheat (*Triticum aestivum*), and barley (*Hordeum vulgare*) because of the extensive work accomplished to date and the successful integration of allelopathy and competition research in these crops.

In order to successfully improve a trait through breeding, there must be variation in the trait among available germplasm, and the trait must be heritable; that is, a significant portion of the observable phenotypic variation expressed among genotypes must be attributed to genotypic differences (Fehr et al., 1987). Furthermore, any released lines will have to yield comparably well to commercial cultivars and meet all other agronomic and market requirements. Courtois and Olofsdotter (1998) suggested that scientists need to establish good screening techniques, verify the existence of genetic variability for weed suppressive ability in available germplasm, and understand genetic control of weed suppressive traits in order to develop appropriate breeding programs.

Much progress has been made to identify allelochemicals and biochemical mechanisms of allelopathy (see Belz, 2007 for review). While such research is important to further the field, this review is focused on plant breeding for weed suppression. Specifically, we review field and laboratory screening protocols, genetic studies, and breeding efforts that have been undertaken to improve allelopathy and competitive ability in cereal crops. We conclude with a discussion of potential methods to optimize research efforts and to move weed suppressive crops out of the laboratory and into farmers’ fields.

Screening Methods

When beginning a new breeding program researchers must first decide how to screen germplasm for weed suppressive ability in order to select promising parent material. The obvious choice is to conduct initial trials in weedy field conditions, but environmental variation and genotype by

environment interactions can make efficient phenotypic selection difficult (Coleman et al., 2001). Furthermore, allelopathy and competition function together to suppress weeds and are virtually impossible to distinguish between in field studies (Inderjit and delMoral, 1997). Laboratory or greenhouse bioassays controlling for genotypic variation in competition for light, water, and nutrients should be considered as an initial screening tool, or supplement for allelopathic research, in order to identify lines that may lack competitive traits but possess superior allelopathic activity.

Ultimately, a breeding program for allelopathy must include both field and laboratory components to make genetic gains. However, lines with superior competitive ability usually can be evaluated and selected in the field alone. Field studies often have complications even when allelopathy is not considered, but if the effects of competition or allelopathy are not observable in the field, then they are ultimately not worth the effort or resources of breeders.

Field Screening for Weed Suppression Rice cultivars and accessions have been screened for weed suppressive ability in field trials conducted in Arkansas (Dilday et al., 1991, 1994), Australia (Seal et al., 2008), the Philippines (Courtois and Olofsdotter, 1998), China (Chen et al., 2008; Kong et al., 2011), Africa (Fofana and Rauber, 2000), and Cambodia (Pheng et al., 2009b) (Table 1). Wheat lines have been tested for weed suppressive ability in Australia (Lemerle et al., 1996, 2001a), Canada (Mason et al., 2007, 2008), India (Balyan et al., 1991), Germany (Verschwele and Niemann, 1993) Sweden (Bertholdsson, 2005, 2010, 2011), the U.S. (Wicks et al., 1986, 2004), and the U.K. (Seavers and Wright, 1999) (Table 1). Barley lines have been tested for weed suppression in the field in Australia (Paynter and Hills, 2009), Brazil (Galon et al., 2011), Canada (O'Donovan et al., 2000; Watson et al., 2006), Denmark (Christensen, 1995), and Sweden (Bertholdsson, 2004, 2005, 2007) (Table 1). In each study, the field experiments were designed differently depending on the specific research objectives and available resources. Although there is no one correct experimental design, we present some of the choices, tradeoffs, and limitations that researchers must make, and we present suggestions to optimize research outcomes. Lemerle et al. (2001b) presents a thorough review of experimental designs for evaluating weed suppressive ability in wheat.

Some researchers hoping to screen cultivars or breeding lines for weed suppressive ability have used natural weed populations (Dilday et al., 1991; Fofana and Rauber, 2000; Mason et al., 2007), while others have overseeded plots with a selected weed species (Coleman et al., 2001; Lemerle et al., 2001a). Although natural weed populations may be more relevant to conditions in farmers' fields and provide evidence of suppressive activity against several important weeds, it may be difficult to achieve uniform weed densities

and therefore to obtain good estimates of weed suppressive ability. Even in experiments where weeds are directly seeded, obtaining uniform weed densities is sometimes problematic. Therefore, Cousens and Mokhtari (1998) used crop establishment counts as a covariate to control for differences across plots.

Weed density also may influence the effectiveness of screening breeding lines for weed suppressive ability (Cousens and Fletcher 1990). Lemerle et al. (2001b) suggested that densities of at least 400–500 rigid ryegrass (*Lolium rigidum*) plants were necessary to show differences in wheat yield under weedy conditions. Other research have indicated that lower seeding rates also may be acceptable as varietal rankings for weed suppressive ability remain constant across seeding rates (Cousens and Fletcher 1990). Researchers must strive to create a level of weed infestation representative of farmers' fields, while maintaining a weed pressures that are sufficient to discern differences in competitive ability among genotypes.

Studies on weed suppressive ability in wheat typically are conducted in weedy plots with no herbicide treatment. However, many rice weed suppression studies have employed fewer applications or lower herbicide rates to give the crop a competitive advantage against weeds. USDA researchers in Arkansas routinely sprayed barnyardgrass with a quarter rate of propanil to give crop plants a competitive advantage and enable the detection of genotypic differences in competitive ability (Gealy et al., 2003, 2005a, b; Gealy and Moldenhauer, 2012; Gealy and Yan, 2012). Similarly, (Kong et al., 2011) tested suppressive lines combined with low-dose bensulfuron methyl (25 g ai ha⁻¹). In studies of rice competition for smallholders in the developing world, single hand-weedings early in the growing season were used to reduce weed pressure to levels where rice accessions expressed differential weed suppressive abilities (Fofana and Rauber, 2000; Pheng et al., 2009b).

Environmental variance and genotype by environment interactions can obscure genotypic differences in weed suppressive ability and hinder phenotypic selection (Coleman et al., 2001). For example, Gealy and Yan (2012) found that barnyardgrass suppression of their most competitive accession was 1.3–1.5 times greater than in commercial long grain rice cultivars, but genotypic differences were non-significant. The power to detect significant differences among cultivars was hindered by high levels of environmental variance within the study location and the small quadrat area used to obtain biomass estimates. Varietal rankings for weed suppressive ability often are inconsistent across growing seasons (Seavers and Wright, 1999) and study locations (Mokhtari et al., 2002), indicating strong genotype by environment interactions. Screening must, therefore, be conducted in multiple growing environments and years to obtain valid estimates of the weed suppressive ability of lines.

Table 1 Location of research programs breeding rice, wheat, and barley germplasm for improved weed suppressive ability and screening germplasm for weed suppressive ability in the field and allelopathy in controlled bioassays

Crop	Location	Germplasm screening		
		Field evaluation	Allelopathy bioassay	Breeding programs ^a
Rice	Australia	Seal et al., 2008	Seal et al., 2008; Seal and Pratley, 2010	
	Cambodia	Pheng et al., 2009b	Pheng et al., 2009a	
	China		Zhang et al., 2005 ^b ; Zhou et al., 2007 ^b ; He et al., 2012	Chen et al., 2008; Kong et al., 2011
	Egypt	Hassan et al., 1994, 1998		
	Japan		Fujii, 1992; Ebana et al., 2001 ^b	
	Korea		Kim et al., 2005; Lee et al., 2008 ^b	Ma et al., 2006
	Philippines	Olofsdotter et al., 1999; Zhao et al., 2006a, b	Navarez and Olofsdotter, 1996; Olofsdotter et al., 1999; Jensen et al., 2001 ^b , 2008 ^b	
	Taiwan		Chou et al., 1991	
	West Africa	Johnson et al., 1998; Fofana and Rauber, 2000		Jones et al., 1997
	U.S. (Arkansas)	Dilday et al., 1991, 1994; Gealy et al., 2003;		Gealy et al., 2005a, b, 2010; Gealy and Moldenhauer, 2012; Gealy and Yan, 2012; Gealy et al., 2013
Spring wheat	U.S. (California)	Gibson et al., 2003		
	Australia	Lemerle et al., 1996; Cousens and Mokhtari, 1998; Lemerle et al., 2001a; Vandeleur and Gill, 2004	Wu et al., 2000a, b, 2003 ^b	Coleman et al., 2001 ^b ; Mokhtari et al., 2002 ^b
	Canada (Saskatchewan)	Huel and Hucl, 1996		
	Canada (Alberta)	Mason et al., 2007, 2008		
	Sweden	Bertholdsson, 2005;	Bertholdsson, 2005, 2007	Bertholdsson, 2010
Winter wheat	U.S. (Washington)	Murphy et al., 2008		
	Argentina	Acciaresi et al., 2001		
	Canada (Alberta)	Blackshaw, 1994		
	Chile		Niemeyer and Jerez, 1997	
	Germany	Verschwele and Niemann, 1993; Drews et al., 2009		
	India	Balyan et al., 1991		
	Sweden	Bertholdsson, 2011	Bertholdsson, 2011; Bertholdsson et al., 2012 ^b	
	United Kingdom	Champion et al., 1998; Seavers and Wright, 1999; Korres and Froud-Williams, 2002		
Spring barley	U.S. (Nebraska)	Challaiah et al., 1986; Wicks et al., 1986, 2004		
	Australia	Paynter and Hills, 2009		
	Canada (Alberta)	O'Donovan et al., 2000		
	Canada (Manitoba)	Watson et al., 2006		
	Denmark	Christensen, 1995		
Winter barley	Sweden	Bertholdsson, 2005;	Bertholdsson, 2004, 2005, 2007	
	Brazil	Galon et al., 2011		
	United Kingdom	Seavers and Wright, 1999		

^a Only research programs crossing cereal lines with the intention of developing progeny with improved weed suppressive ability and testing those progeny in the field are listed as breeding programs

^b These papers describe research focused on determining the genetic architecture of allelopathy or weed suppression

The number of replications and locations that can be tested is limited by the time and labor required to measure weed biomass at the end of the season. Weed biomass generally is cut from a randomly placed quadrat and separated from crop biomass by hand to obtain ratings of weed suppressive ability. To compensate for the time required to cut and separate biomass from each plot, researchers have used fewer replicates or cut very small quadrats (usually less than 1 m²). Bertholdsson (2005) measured weed suppression by sampling a 0.25 m² area of weed biomass in each plot, for example, and found high standard errors between replications.

Counting weed reproductive structures instead of sorting biomass may be a more efficient means of screening lines for weed suppressive ability. Wilson (1988) and Korres and Froud-Williams (2002) found a positive linear relationship between weed biomass m⁻² and reproductive structures m⁻² for a number of important broadleaf and annual grass weeds of winter wheat. Counts of seed heads or reproductive structures may be a more informative measure of weed suppressive ability because they have a direct impact on the weed seed bank in the following season. Visual ratings of weed suppression have been in rice used to evaluate genotypic differences in weed suppressive ability (Dilday et al., 1991, 1994), but a strong suppressive effect is necessary to differentiate suppressive cultivars from non-competitive types.

The high number of replicates involved and labor intensive procedure required for rating weed suppression in the field necessitates evaluating a limited number of genotypes. While some studies screen a large number of genotypes for weed suppression (Dilday et al., 1991; Hassan et al., 1998; Lemerle et al., 2001a), most evaluate less than 100 (Challaiah et al., 1986; Bertholdsson, 2005, 2011), and many less than 10 (Verschwele and Niemann, 1993; Johnson et al., 1998; Seavers and Wright, 1999; Gealy and Moldenhauer, 2012). Johnson et al. (1998) noted that the labor requirements and plot sizes required to screen genotypes for weed suppression limited their ability to evaluate a large amount of material and to identify the most promising lines.

Identification of Competitive Traits

Competitive ability is conferred by a combination of morphological traits that allow the crop to access more limited resources than neighboring weeds. Understanding what traits are most strongly associated with competitive advantages enables breeders to indirectly select for weed suppressive lines in weed free environments, allowing them to screen their entire breeding nurseries (Gibson et al., 2003; Zhao et al., 2006a, b; Bertholdsson, 2011). If the product of the heritability of a specific competitive trait and its correlation with the weed biomass suppression of a cultivar is greater than

the heritability of weed suppression, then indirect selection will be more efficient than direct selection for weed suppressive ability (Falconer, 1981; Gallais, 1984). Even if indirect selection is less effective than direct selection for weed suppressive ability, breeders still may be able to screen their entire weed free nurseries and judiciously choose lines that are likely to have superior weed suppressive ability. These selected lines subsequently can be evaluated in smaller trials where cultivars are overseeded with weeds. Researchers have identified several traits associated with superior competitive ability in wheat, barley, and rice, including end of season cultivar height (Challaiah et al., 1986; Blackshaw, 1994; Huel and Hucl, 1996; Lemerle et al., 1996; Coleman et al., 2001; Vandeleur and Gill, 2004; Mason et al., 2007; Murphy et al., 2008; Gealy and Moldenhauer, 2012), tillering capacity (Challaiah et al., 1986; Blackshaw, 1994; Lemerle et al., 1996; Coleman et al., 2001; Korres and Froud-Williams, 2002; Wicks et al., 2004; Mason et al., 2007, 2008), leaf angle and canopy structure (Huel and Hucl, 1996; Lemerle et al., 1996; Seavers and Wright, 1999; Korres and Froud-Williams, 2002; Drews et al., 2009), early vigor (Wicks et al., 1986; Huel and Hucl, 1996; Acciaresi et al., 2001; Lemerle et al., 2001a, b; Zhao et al., 2006a; Mason et al., 2007), and time to maturity (Huel and Hucl, 1996; Mason et al., 2007).

Selecting a Competitive Ideotype Olofsson et al. (2002) suggested that breeders should select for a competitive 'ideotype' with a combination of several morphological traits associated with competitive ability. Donald and Hamblin (1976) proposed that a competitive wheat ideotype was taller, high tillering, had extensive leaf display, and yielded well in mixture and poorly in monoculture. Weed suppressive rice lines in West Africa accumulated more biomass, produced more tillers, and had a higher Leaf Area Index (LAI) (Johnson et al., 1998). Huel and Hucl (1996) found that the most tolerant spring wheat genotypes in western Canada had high biomass and long flag leaves, good ground cover, and were tall. Other Canadian spring wheat breeders found that taller lines with fast early season growth, early maturity, and greater number of fertile tillers had the most competitive ideotype (Mason et al., 2007). In contrast, Coleman et al. (2001) found that the most competitive wheat genotypes in Australia had tall final height and good early vigor, but were late maturing and had shorter shoot length at stem extension. It is clear that no one ideotype is appropriate for every environment. Different combinations of traits will confer the greatest competitive advantage to grain cultivars depending on the growing season climatic conditions, weed species of importance, and timing of competition.

The most competitive plants also will have good biotic and abiotic stress resistance (Olofsson et al., 2002). Wicks et al. (2004) found that Siouxsland, a tall cultivar that was

previously shown to compete well against weeds, was a poor suppressor during a severe leaf rust epidemic owing to its susceptibility. Winter hardiness also contributed to weed suppressive ability among winter wheat cultivars in Nebraska (Wicks et al., 2004). Cousens and Mokhtari (1998) measured the tolerance of 17 spring wheat cultivars overseeded with rigid ryegrass in multiple years and locations across Australia. The performance of the cultivars was erratic across environments; only one cultivar was consistently ranked as tolerant in all study locations. Timing of drought might have influenced competitive traits differentially across environments; early maturing lines performed better in environments with low water availability late in season (Mokhtari et al., 2002). Lemerle et al. (2001a) also found that rankings of the most competitive genotypes of Australian wheat were inconsistent across environments. The correlation between weedy and weed free yield was high, suggesting that local adaptation was important for competitiveness (Lemerle et al., 2001a). A decentralized approach to breeding, thus, may be appropriate for weed suppressive ability. Breeders in each major production region will need to conduct pilot trials to determine the traits that confer the most competitive advantage to crop cultivars and screen adapted material that meets agronomic criteria and performs well in the target environment.

When choosing traits appropriate for indirect selection, breeders must consider the heritability of those traits and practical constraints to obtaining these data. Rapid gains from selection could be obtained by selecting for high heritability traits such as early vigor, height, and time to maturity. Many traits that have been implicated in competitive interactions (such as tiller counts and root traits) cannot be practically measured or selected for in breeding programs with thousands of field plots. Destructive measurements such as early biomass production are also inappropriate for indirect selection because they are time consuming to measure and prevent the researcher from evaluating other traits. Such measurements may be appropriate if they could be estimated with a visual rating or obtained with tools such as non-imaging spectrophotometers.

Genetics of Competitive Ability

An understanding of the genetics of competition can help researchers design appropriate breeding schemes and enable Marker Assisted Selection (MAS). Weed suppressive ability and tolerance have been normally distributed in progeny from crosses between competitive and non-competitive grain cultivars, indicating a quantitative mode of inheritance and control by a number of genes with moderate to minor effects (Coleman et al., 2001; Mokhtari et al., 2002).

Mokhtari et al. (2002) scored tolerance in two $F_{2:3}$ populations; one derived from a cross between locally adapted Australian wheat cultivars with early flowering dates, and the other from a cross between late flowering cultivars. Utilizable levels of genetic variation for tolerance were found in adapted material, and the narrow-sense heritability for tolerance was estimated at 0.25 and 0.57 on an entry mean basis in the early and late crosses, respectively. In the early cross, the relative efficiency of indirect selection for number of seed heads per plant and total dry weight in monoculture was greater than direct selection. No morphological traits measured in the late cross had the combination of high heritability and correlation with tolerance necessary to achieve greater efficiency than direct selection (Mokhtari et al., 2002).

In a trial measuring heritability and potential for indirect selection in 40 upland rice cultivars over 3 years, Zhao et al. (2006a) predicted an entry mean broad-sense heritability of 0.79 for weedy yield and 0.64 for weed biomass. Zhao et al. (2006b) also found high broad sense heritabilities for visual ratings of early vigor (0.88) and height (0.81) 4 weeks after seeding. Height ($r=-0.93$) and vigor rating ($r=-0.59$) 4 weeks after seeding were also strongly, but negatively correlated with weed biomass at 13 weeks after seeding, making them good candidates for indirect selection (Zhao et al. 2006b).

Coleman et al. (2001) found that the entry mean narrow-sense heritability of morphological traits associated with weed suppressive ability varied significantly; flowering date was estimated at 0.99, height at stem elongation at 0.90, tiller number at 0.34, leaf area index during stem extension at 0.18–0.31, and crop dry matter during tillering at 0.18. Heritability estimates depended on the population being studied and the experimental conditions. Based on these results, we can conclude that weed suppressive ability is a moderately heritable trait and that indirect selection for morphological traits associated with superior competitive ability in weed-free plots may be advantageous in some instances.

Zhang et al. (2005) investigated the genetic control of early vigor traits including seedling germination, shoot length, and dry matter weight in a population derived from a cross between a weed suppressive indica rice line and a non-weed suppressive japonica cultivar. Thirteen quantitative trait loci (QTL) were identified, each controlling 5–10 % of variation in components of early vigor. Coleman et al. (2001) also identified QTL associated with important morphological traits implicated in weed competition in a double haploid mapping population. Time to anthesis, flag leaf size, height at stem elongation, and size of first two leaves were mapped to similar positions on chromosomes 2B and 2D in both years of the study. The position of the locus associated with time to anthesis on chromosome 2D suggested that it could be a photoperiod insensitivity gene. Height at anthesis was controlled by a locus at 4B corresponding to the position of dwarfing gene *Rht-B1b*

(Coleman et al., 2001). However, given that different traits appear to confer weed suppressive ability in different environments, each research group should conduct separate QTL analysis to find the genomic regions associated with weed suppressive ability in their own populations. The identification of QTLs associated with weed suppression can further breeding activities through the discovery of molecular markers closely linked with genes that control traits for selection. Those markers then can be incorporated into MAS activities that can increase the efficiency of selection and breeding (Paterson et al., 1988).

Marker assisted selection is likely to be particularly beneficial in increasing early vigor in wheat. Taller historical cultivars, lacking modern dwarfing genes, have shown superior weed suppressive ability. However, very tall wheat cultivars are undesirable because of their susceptibility to lodging and low harvest index (Murphy et al., 2008). The dwarfing genes *Rht-B1b* and *Rht-D1b*, which are present in most modern wheat cultivars, confer reduced final cultivar height and also suppress early vigor and sensitivity to gibberellic acid. Research on breeding for early vigor in Australia has suggested that alternate dwarfing genes, such as *Rht-8*, may reduce final cultivar height without reducing early vigor (Rebetzke and Richards, 1999). Thus, wheat cultivars with alternate dwarfing genes could be good suppressors of weeds. Addisu et al. (2009) grew wheat lines with different dwarfing genes in organic and conventional production systems and found that genotypic differences in yield and weed suppression were exaggerated in organic conditions. Reduced height gene *Rht-8* was positively associated with winter survival and early season growth, but neighboring photoperiod insensitivity gene *Ppd-D1a* had an even stronger effect on early vigor (Addisu et al., 2009). Worland (1996) identified genes controlling flowering time including vernalization genes on the group 5 chromosomes, photoperiod genes on the group 2 chromosomes, and earliness *per se* genes throughout the genome. Closely linked markers are available for many dwarfing, vernalization, and photoperiod genes (Graingenes wheat.pw.usda.gov/). Further research is needed to determine the importance of these genes to weed suppressive ability in different growing environments.

Allelopathy Bioassays

Laboratory bioassays for allelopathy accompanied initial field screenings in rice, and until recently, were the only screening tools used to evaluate allelopathy in wheat and barley (Belz, 2007). The advantages of laboratory or greenhouse bioassays over field screening include the ability to differentiate allelopathic effects from competitive interactions and the increased heritability conferred by controlled settings where environmental variance is minimized

(Coutois and Olofsson, 1998). Olofsson et al. (2002) found that the entry mean narrow-sense heritability estimates of individual allelopathy screening experiments ranged from 0.72 to 0.85, a significant improvement over estimates for weed suppressive ability in the field. Jensen et al. (2008) reported that entry mean broad-sense heritability estimates for rice allelopathy depended on the screening method used and ranged from 0.71 for barnyardgrass root length inhibition in 'relay seeding' assays, to 0.74 and 0.43, respectively, for barnyardgrass shoot and root biomass reduction in pot screening assays conducted in the greenhouse.

Screening bioassays must be inexpensive, convenient, rapid, reproducible, and simple to operate to be practical for plant breeding (Wu et al., 2001). When choosing a screening technique, researchers must balance the need to effectively distinguish between allelopathy and other forms of plant-plant interaction and the benefits of representing natural conditions as closely as possible (Inderjit and Olofsson, 1998). Wu et al. (2001) presented a thorough review of the available screening methods for evaluating crop allelopathic potential. Seedling screening bioassays including the 'plant-box method' (Fujii, 1992), the 'relay-seeding technique' (Navarez and Olofsson, 1996), the 'equal-compartment-agar-method' (Wu et al., 2000b), and hydroponic methods (Belz and Hurle, 2004; Kim et al., 2005; He et al., 2012) have been popular techniques for allelopathy research. In such bioassays, seedlings of the crop (donor) species generally are grown with seedlings of weed (receiver) species for a specified period of time. Allelopathic potential then is measured as depressed receiver root or shoot development, as compared to a control (where the receiver is grown in the absence of any donor species).

Rice cultivars do not appear to have consistent allelopathic activity against multiple families of weeds (Dilday et al., 1991, 1998; Hassan et al., 1994, 1998; Navarez and Olofsson, 1996; Olofsson et al., 1999; Seal et al., 2008; Seal and Pratley, 2010). However, many rice cultivars may be able to inhibit the growth of several related species of weeds (Seal and Pratley, 2010). Seal and Pratley (2010) tested the allelopathic potential of 27 rice lines against barnyardgrass and a number of endemic Australian weeds from the Alismataceae family using the 'equal compartment agar method.' The seven most suppressive cultivars reduced weed root growth by over 90 %, while non-allelopathic cultivar Langi actually stimulated barnyardgrass root growth by 20 %. A few cultivars were allelopathic against the whole spectrum of weed species tested, but others were able to suppress the growth of only one or a few weed species. Correlation between allelopathic activity against barnyardgrass and giant arrowhead (*Sagittaria montevidensis*) was lowest ($r=0.58$), reflecting the observance that allelopathic potential rarely extends to multiple families of weeds. However, correlation between allelopathic activity against grassy arrowhead (*Sagittaria graminea*) and lance-leaved

water plantain (*Alisma lanceolatum*) was 0.93, indicating that allelopathic potential was relatively consistent within weed families. Allelopathic activity in wheat and barley may be effective against a wider range of weed species. Bertholdsson (2005) found similar results when screening spring wheat and barley cultivars for allelopathic potential using oilseed rape (*Brassica napus*) and perennial ryegrass (*Lolium perenne*) as receiver species in the 'equal compartment agar method'. However, in a subsequent study, Bertholdsson (2011) found that the potential allelopathic activity of winter wheat cultivars against mustard (*Sinapis alba*) and perennial ryegrass receiver species was not correlated ($r=0.09$, ns), and that only allelopathic activity against mustard was correlated with weed suppression in the field. These findings highlight the importance of using locally relevant, economically important weeds as receiver species and testing for allelopathic effects against multiple problematic species.

Variation in Allelopathy Within Available Germplasm In addition to choosing screening techniques, researchers must choose which cultivars and accessions to evaluate. In order to improve allelopathy through breeding, researchers must first identify variation in the allelopathic potential of available germplasm (Courtois and Olofsdotter, 1998). Harlan and deWet (1971) introduced the idea of primary, secondary, and tertiary gene pools, where the primary gene pool includes the lines of the cultivated species, the secondary gene pool includes related species that will hybridize with cultivated lines, and the tertiary gene pool includes more distantly related species in the genus. If useful genetic variation exists within the species, especially within genetic material adapted to the production region of interest, then screening material from secondary or tertiary gene pools may be unnecessary. Putnam and Duke (1974) suggested that allelopathy may be lower in cultivated species than wild relatives, due to an absence of positive selection and genetic bottlenecks during domestication. Therefore, crop wild relatives and ancestral species may possess high allelopathic potential that could be useful in breeding programs.

Despite suggestions that breeding programs may have inadvertently selected against allelopathy in weed free nurseries, studies that track allelopathy in historical cultivars are inconclusive. Allelopathic activity has declined in barley (Bertholdsson, 2004) and slightly increased in spring wheat (Bertholdsson, 2007) during the past century of breeding activities. Traditional rice accessions generally are more allelopathic than modern cultivars in some studies (Fujii, 1992), while modern cultivars are more allelopathic than older releases in others (Courtois and Olofsdotter, 1998). Based on these results, it may be worthwhile to screen both older and newer cultivars for allelopathy to identify the most promising sources of breeding materials.

Rice diversity is strongly bipolar due to a diphyletic pattern of domestication (Second, 1985). Global rice accessions have been sorted into five groups by using SSR markers where temperate japonica, tropical japonica, and aromatic groups comprise the japonica subspecies, while indica and aus groups are contained in the indica subspecies (Garris et al., 2005). A related species, *Oryza glaberrima*, is grown in upland production systems in West Africa. While some researchers have found a higher incidence of allelopathy in tropical japonica accessions (Fujii, 1992; Courtois and Olofsdotter, 1998) and *O. glaberrima* (Fujii, 1992), others have found promising allelopathic accessions within indica germplasm (Gealy and Moldenhauer, 2012; Gealy and Yan, 2012). Tropical japonica cultivars are common in drill seeded rice in the southern U.S., but field screenings for allelopathy in Arkansas have shown that indica lines and a few commercial hybrids consistently suppress weeds more effectively than local material (Gealy et al., 2005a, b; Gealy and Moldenhauer, 2012). Gealy and Moldenhauer (2012) found that weed suppressive indica cultivars provided 30 % better control of barnyardgrass and suffered 44 % less yield loss than non-suppressive tropical japonica cultivars representative of current U.S. production. A high incidence of allelopathy also was observed in *O. rufipogon*, a wild relative of cultivated rice, in a controlled bioassay with *Brassica oleracea* as a receiver species (Chou et al., 1991).

Genetics of Allelopathy

Marker Assisted Selection Research on the genetics of allelopathic cultivars has received less attention than other areas of allelopathy science (Wu et al., 1999), but much progress has been achieved in the past decade. In a bioassay of 453 winter wheat cultivars from around the world, Wu et al. (2000a) found a normal distribution of allelopathic activity, indicating a quantitative mode of inheritance. Allelopathic activity was normally distributed in the progeny derived from crosses between strongly and weakly allelopathic lines in wheat (Wu et al., 2003; Bertholdsson, 2010) and rice (Ebana et al., 2001; Jensen et al., 2001, 2008; Zhou et al., 2007; Chen et al., 2008). The narrow range of weeds controlled by certain allelopathic cultivars suggested that several chemical compounds were conferring allelopathy against different weed species (Courtois and Olofsdotter, 1998). Multigenic control was further indicated by the probable activity of more than one phytotoxin controlling allelopathic outcomes. Wu et al. (2000a) also studied allelopathy in backcross populations of the near isogenic lines Hartog (a non-allelopathic line) and Janz (an allelopathic line). They found that BC₂ Hartog lines were weakly allelopathic while BC₂ Janz lines were strongly allelopathic,

providing further evidence that there was a genetic basis to allelopathy (Wu et al., 2000a).

A few efforts have been made to map allelopathy genes in wheat (Niemeyer and Jerez, 1997; Wu et al., 2003). Wu et al. (2003) used restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), and simple sequence repeat (SSR) markers to map allelopathy QTLs in a double haploid (DH) population derived from a cross between Australian cultivars Sunco (moderately allelopathic) and Tasman (strongly allelopathic). Researchers identified two major QTLs associated with allelopathy on wheat chromosome 2B, based on the 189 DH lines and two parents (Wu et al., 2003). Niemeyer and Jerez (1997) mapped the location of genes controlling hydroxamic acids, which are probable allelochemicals in wheat. The mapping population was constructed from crosses between cultivar Cheyenne and substitution lines derived from Chinese Spring, a cultivar with high hydroxamic acid. QTLs controlling hydroxamic acid accumulation were identified in chromosomes 4A, 4B, 4D, and 5B (Niemeyer and Jerez, 1997).

More extensive allelopathy QTL mapping experiments have been conducted in rice. Ebana et al. (2001) used RFLP markers to map QTLs controlling allelopathy in an F₂ population developed from PI 312777, a highly allelopathic accession, and Rexmont, a low allelopathy long grain rice cultivar grown in the southern U.S. Allelopathy was measured by collecting water soluble leaf extracts from rice plants at the six leaf growth stage and measuring root length inhibition in lettuce (*Lactuca sativa*) and ducksalad (*Heteranthera limosa*) seedlings watered with these extracts. Seven allelopathy QTLs were identified on chromosomes 1, 3, 5, 6, 7, 11, and 12. The largest single QTL on chromosome 6 explained 16 % of the total phenotypic variation, and a multiple QTL model estimated that the five most important QTLs explained 36.6 % of phenotypic variation when considered jointly (Ebana et al., 2001). Jensen et al. (2001) used a population of 142 recombinant inbred lines derived through single seed descent from a cross between IAC165, an allelopathic japonica upland rice cultivar from Brazil, and CO39, a weakly allelopathic indica cultivar from India to map allelopathy QTLs in rice. ‘Relay seeding’ assays showed transgressive segregation in both directions among the progeny, indicating that even CO39 had some allelopathic activity. Four main effect QTLs on chromosomes 2, 3, and 8 explained 35 % of the phenotypic variation observed in the population (Jensen et al., 2001). To confirm the effects observed in the IAC165 x CO39 population, Jensen et al. (2008) developed a new mapping population specifically designed to identify QTLs conferring allelopathic potential. The population was derived from a cross between allelopathic indica cultivar AC1423 and non-allelopathic cultivar Aus196 and tested

for allelopathic activity against barnyardgrass by using the ‘relay seeding’ technique and a pot screening experiment in the greenhouse. In the greenhouse experiment, a screen was placed between the halves of the pot containing rice and barnyardgrass seedlings, and a constant supply of adequate nutrients and water was provided to control for genotypic differences in competitive ability. A total of 15 QTLs, each explaining 5–11 % of phenotypic variation, were identified on chromosomes 3, 4, 6, 8, 9, 10, and 12 when considering the results from the ‘relay seeding’ assay and the four allelopathic measurements (barnyardgrass root biomass, root length, shoot biomass, and shoot length) collected in the greenhouse assay (Jensen et al., 2008). Two QTLs on chromosomes 3 and 8 mapped to the same intervals as previously identified QTL reported in Jensen et al. (2001), and many QTLs were located in similar regions to those identified by Ebana et al. (2001). Zhou et al. (2007) also used 147 recombinant inbred lines derived from two Chinese cultivars Zhong-156 (strongly allelopathic) and Gumei-2 (weakly allelopathic) to identify three main-effect QTLs on chromosomes 5 and 11 that explained 13.6 % of phenotypic variation when considered together. In summary, QTLs controlling allelopathy have been identified across the rice genome in every region except chromosome 2.

Studies on the genetic control of allelopathy conducted thus far have been limited by the availability of suitable mapping populations. Considering the wide array of allelopathic compounds that have been identified in crop genotypes and the probable role of regulatory genes in controlling the expression of allelopathy under stress (Einhellig, 1996), association mapping may bring new insight into the genetic control of allelopathy. Association mapping identifies QTLs by examining marker-trait associations that can be attributed to the strength of linkage disequilibrium between markers and functional polymorphisms across a diverse set of germplasm (Zhu et al., 2008). Association mapping provides increased mapping resolution, reduced research time, and greater allele numbers than traditional QTL mapping (Zhu et al., 2008). With the increased availability of single nucleotide polymorphisms (SNPs) and diversity arrays technology (DArT) markers, association mapping has become a viable option for allelopathy researchers. The discovery of additional fine resolution QTLs controlling allelopathy in wheat and rice cultivars will lead hopefully to the development of effective molecular markers that can be used in marker assisted selection for cultivars with improved allelopathic activity.

Marker assisted selection may be hindered because of the large number of minor effect QTLs that appear to control allelopathy in various genotypes. Courtois and Olofsdotter (1998) suggested that Marker Assisted Backcrossing would be a good tool for breeders if fewer than five major QTL control allelopathy. With more QTLs controlling allelopathy,

it becomes increasingly difficult to recover important agronomic characters from a non-allelopathic recurrent parent and retain all the QTLs contributing to allelopathic activity from the donor parent.

Transgenic Approaches Transgenic approaches also have been suggested as potential tools to improve crop allelopathy (Duke et al., 2001; Bertin et al., 2008, see also Duke et al., 2013). However, a clear understanding of the genes involved in the regulation and biosynthesis of allelochemicals is necessary to steer such pathways toward enhanced allelochemical production. While QTL mapping can facilitate MAS, it rarely results in gene discovery. Hundreds of candidate genes can be located within a single QTL spanning 5–10 cM (Bertin et al., 2008). Thus, additional tools generally are required to pinpoint specific causative genes. Genes that control the biosynthesis of allelochemicals can be identified through the discovery, isolation, and purification of plant enzymes and related bioactive metabolites (Yang et al. 2004), activation tagging (Hayashi et al. 1992), and the use of gene knockout libraries (Krysan et al. 1999). Specific genes have been implicated in the biosynthesis and activity of several known allelochemicals including momilactones (Shimura et al. 2007, Xu et al. 2012; see also Kato-Noguchi and Peters, 2013), phenolic compounds (Fang et al., 2009), and benzoxazinoids (Frey et al., 2009; see also Shulz et al., 2013).

Gene overexpression and antisense knockout techniques could be used to alter the quality and quantity of secondary metabolites produced by allelopathic plants. However, despite recent advances, the control points governing the production of rate limiting enzymes in the biosynthetic pathway of allelochemicals generally are not well understood (Bertin et al., 2008). Transgenic approaches also could be used to introduce new allelopathy genes from foreign sources to non-allelopathic crop species. The feasibility of such actions is limited by the complex genetic architecture of allelopathy. A multigene expression system would have to be introduced into the crop and its regulation would need to be optimized so that the transformed crop could successfully produce the desired allelochemicals and localize them in the proper tissue (Bertin et al., 2008).

In addition to the technological and economic barriers stalling the development of genetically modified organisms (GMOs) with enhanced allelopathy, social and political opposition may limit the adoption of these tools. Weed suppressive crops are particularly valuable for organic production systems, which prohibit the use of GMOs. For these reasons, classical plant breeding and MAS are currently the most feasible means of improving allelopathy in crop plants. As biosynthetic pathways controlling allelochemical production become better understood and public perception of GMOs evolves, transgenic approaches may become useful complements to classical breeding efforts (see Pickett, 2012).

Testing Allelopathy in the Field

Olofsdotter et al. (2002) concluded that allelopathy and resource competition cannot be separated under field conditions and selection for allelopathic activity is not a viable option. On the other hand, field screening better predicts the performance of cultivars when deployed in an agricultural setting, and if allelopathic material is not efficacious in the field, breeders' time and resources should be allocated to other activities. Therefore, field screenings and laboratory bioassays should be conducted concurrently to achieve improvements in allelopathic activity.

Allelopathy in rice was first noted by R. H. Dilday in the field while evaluating accessions for alachlor tolerance at the Dale Bumpers Rice Research and Extension Center in Stuttgart, AR, USA in 1985 and 1986 (Dilday et al., 1991). Allelopathy was distinguished from competitive effects based on a distinctive ring surrounding some rice plants wherein weeds were less prevalent or stunted. By 1990, 12,000 global rice accessions had been screened for allelopathic effects against duck salad, and 5,000 for allelopathic activity against redstem (*Ammannia coccinea*) in Arkansas. Four hundred and twelve accessions were identified with allelopathic activity against duck salad, 145 accessions showed allelopathic activity against redstem, and 16 were allelopathic against both duck salad and redstem (Dilday et al., 1998). A breeding program in Egypt screened 1000 accessions against barnyardgrass and smallflower flat sedge (*Cyperus difformis*) in the field (Hassan et al., 1994, 1998). Thirty accessions were effective suppressors of barnyardgrass, 15 cultivars suppressed smallflower flat sedge, and 5 cultivars were suppressive against both weed species. About 3.4 % of material screened in Egypt and Arkansas was allelopathic against at least one weed species in the field, but as in controlled bioassays for allelopathy, cultivars with suppressive ability across a wide spectrum of weeds were rare (Dilday et al., 1998; Hassan et al., 1998; Olofsdotter, 1998). Both programs were conducted in the field, and while the weed free area surrounding rice plants was indicative of allelopathy, these effects were confounded to some extent by competitive traits.

While allelochemicals may behave differently in the soil than they do in nutrient free agar, rice seedlings that are allelopathic in laboratory bioassays also are allelopathic in the field (Navarez and Olofsdotter, 1996; Kato-Noguchi and Peters, 2013). Field and laboratory results were strongly correlated ($r=0.71$) in a test of 23 cultivars that had been screened for allelopathy against endemic Australian weeds and then tested in fields infested with starfruit (*Damasonium minus*) (Seal et al., 2008). Tono Brea 439, the most allelopathic cultivar, suppressed starfruit root length by 97 % in the 'equal compartment agar method' and starfruit dry weight by 95.4 % compared to no-rice controls in the field.

The least suppressive cultivar, Rexmont, suppressed starfruit root biomass by only 67 and 27.8 % in the bioassay and field experiment, respectively.

Olofsdotter et al. (1999) screened 111 rice cultivars for weed suppressive ability using the 'relay seeding' bioassay and replicated field trials. They found that some field suppressive cultivars, such as Taichung Native 1, were highly allelopathic but lacking in traits that contribute to competitive ability, while others, such as Brown Gora, were tall and had good competitive features but insignificant allelopathic activity in laboratory bioassays. Based on regression results from three field seasons, Olofsdotter et al. (1999) concluded that the additive effects of allelopathy and competition controlled weed interference outcomes in the field, and that 34 % of observed rice interference was due to allelopathy. Correlations between allelopathy ratings obtained from the 'relay seeding' bioassay and weed biomass in the field ranged from 0.41 to 0.65 over three seasons (Olofsdotter et al., 1999).

Bertholdsson (2005) used multiple regression to parse the relative contribution of allelopathy and competition to observed weed suppression by barley and spring wheat cultivars in the field. In barley, early crop biomass explained 24 to 57 % variation in weed biomass, while allelopathy explained seven to 58 %, and their combined effects explained 44 to 69 %. Early vigor and allelopathy explained less of the observed variation in the weed suppressive ability of spring wheat cultivars; 14 to 21 % of variation in weed biomass was explained by early biomass, zero to 21 % by allelopathic activity, and 27 to 37 % through their combined activity. Based on these results, models were constructed that predicted that a 20 % improvement in wheat allelopathy would cause a corresponding decrease in weed biomass of eight to 15 %. In a subsequent study, Bertholdsson (2011) used multivariate statistics to separate allelopathy and competitive factors in winter wheat. The weed suppressive ability of 12 winter wheat, two rye, and two triticale cultivars was measured in fields overseeded with oilseed rape and loose silkybent (*Apera spica-venti*). Early season crop biomass and allelopathy were the two traits that explained the most variation. Least squares predictions indicated that weed biomass could be decreased by 60 % if allelopathy and early vigor in winter wheat could be improved to the level of rye (Bertholdsson, 2011).

Environmental Effects on Allelopathic Activity Breeding efforts for improved allelopathic potential are further complicated by environmental effects on trait expression (Dilday et al., 1998; Olofsdotter et al., 1999). Solar irradiation, mineral deficiencies, water stress, temperature, and rhizosphere organisms can all impact the expression of allelopathy (Rice, 1984). Dilday et al. (1998) found that year to year variation, soil type, weed density, rice plant number, rice root development, and root density also affected allelopathic

activity in the field. Highly allelopathic spring wheat lines derived from a cross between allelopathic and non-allelopathic parents suppressed weed biomass 24 % more than the non-allelopathic parent in the dry year and only 12 % more in the wet year (Bertholdsson, 2010). However, Courtois and Olofsdotter (1998) found that changes in water status and soil organic matter content did not affect the general allelopathy rankings of upland rice genotypes.

Many rice lines scored as allelopathic in Arkansas did not significantly affect weed growth when grown in the Philippines (Olofsdotter et al., 2002). The cultivar Dular previously was described as allelopathic against barnyardgrass and smallflower flat sedge in Egypt (Hassan et al., 1994) and non-allelopathic against ducksalsad in Arkansas (Dilday et al., 1991). However, Seal and Pratley (2010) found that Dular had intermediate allelopathic effects against the Alismataceae species and poor allelopathic potential against barnyardgrass in Australia. Giza 176 was notably non-allelopathic against barnyardgrass and smallflower flat sedge in Egypt (Hassan et al., 1994), but it was among the most allelopathic lines when tested against barnyardgrass and Alismataceae weeds in controlled bioassays and field trials in Australia (Seal and Pratley, 2010). The observed discrepancies in the findings of these breeding programs could be due to differences in experimental design, but more likely because of genotype by environment interactions.

Cultivar Development

A breeding program can be launched when all essential conditions are met, including 1) the identification of a good screening technique, 2) the discovery of genetic variability for this trait in available germplasm, and 3) an understanding of genetic control of the trait (Courtois and Olofsdotter, 1998). Rice allelopathic potential is not correlated with cultivar height (Olofsdotter and Navarez 1996), root biomass (Jensen et al., 2001), or any other competitive trait (Olofsdotter et al., 1999). Similarly, wheat allelopathic potential was not correlated with thousand grain weight, plant height, or root length of wheat seedlings (Wu et al., 2000a). Thus, it should be possible simultaneously improve competitive ability and allelopathy.

Breeding Weed Suppressive Rice in Arkansas The high incidence of allelopathy in rice cultivars can be attributed partially to the indica line Taichung Native 1 (TN-1), which is strongly allelopathic against barnyardgrass, ducksalad, redstem, and desert horse purslane (*Trianthema portulacastrum*) (Olofsdotter and Navarez 1996; Dilday et al., 1998). TN-1 was widely used as a parent in the International Rice Research Institute (IRRI) breeding programs, and consequently,

is in the genetic background of many modern cultivars. One particularly allelopathic accession, PI 312777, was developed in the Philippines from a cross between Taichung 65*2 and TN-1 (Gealy et al., 2005a, b). PI 312777 has been identified as allelopathic and weed suppressive in controlled bioassays (Kong et al., 2011) and field trials in Arkansas (Dilday et al., 1994), and Asia (Olofsdotter et al., 2002; Chen et al., 2008; Kong et al., 2011). In Arkansas, grain yield reduction relative to weed free plots was 1.6 times greater in Kaybonnet, a locally adapted cultivar, than PI 312777, indicating that PI 312777 has excellent tolerance as well as weed suppressive ability (Gealy and Moldenhauer, 2012). Unfortunately, PI 312777 is not suited for production in the U.S. due to lodging susceptibility and poor milling yields (Gealy and Moldenhauer, 2012).

Asian indica accessions, such as PI 312777, generally are more weed suppressive than commercial southern long grain cultivars, but the quality of these lines does not meet U.S. industry standards (Gealy et al., 2003). Thus, the USDA rice breeding program in Arkansas sought to combine quality and yield characteristics from southern long grain cultivars with weed suppression from competitive indica lines. Beginning in 1991, the moderately allelopathic indica accession PI 338046, which had better milling yield than PI 312777, was hybridized with several commercial U.S. cultivars (Dilday et al., 1998). Seven F₆ generation lines were derived from each cross by using single seed descent, and evaluated for allelopathic effects on duck salad in a greenhouse experiment and for milling yield, heading date, plant height, and lodging susceptibility in field trials (Dilday et al., 1998). A promising line, RU9701151, was selected from the cross between PI 338046 and Katy based on its acceptable milling yields, plant type, and cooking quality (Moldenhauer et al., 1999).

Unfortunately, crosses between weed suppressive indica accessions and locally adapted *japonica* cultivars generally yielded progeny with intermediate allelopathy and weed suppression (Gealy et al., 2005a, b). To recover better weed suppression, lines derived from PI 338046 and local cultivars were crossed with allelopathic accession PI 312777. Twelve F₅ derived lines derived from the cross PI338046/Katy//PI 312777 then were developed via single seed descent and tested in replicated yield trials. Of the 12 lines tested, 10 had 60 % weed control or better compared to neighboring plots with no rice, 10 had acceptable yields in weed-free plots (6,500 kg·ha⁻¹ or better), and 11 had grain yields within 70 % of their weed free check plots (Gealy et al., 2005a, b).

STG06L-35-061 (a particularly promising line with a pedigree containing PI 330846, PI 312777, Katy, and Drew) was identified as weed suppressive in field trials in 2008 (Gealy et al., 2010). The weed suppressive ability of STG06L-35-061 has been nearly as strong as PI 312777 in some tests. Furthermore, this line yielded competitively with commercially available southern long grain cultivars and

resisted lodging. The results of a seedling bioassay conducted in a growth chamber indicated that the allelopathic activity of STG06L-35-061 was intermediate between PI 312777 and Katy (Gealy et al., 2010). STG06L-35-06 currently is being evaluated in advanced breeding trials and is being considered for a possible germplasm release (Gealy et al., 2013).

Another cultivar, Rondo, (4484–1693; PI 657830) is being recommended for its weed suppressive ability. Rondo is a high yielding indica line from Asia that was developed by using mutation breeding (Yan and McClung, 2010). Rondo is less prone to lodging than its parent, has higher amylose content, is resistant to all major races of rice blast (*Magnaporthe grisea*) common in the U.S., and yields competitively with elite U.S. cultivars (Yan and McClung, 2010). Rondo, a sister line (4485–1665), and other indica rice lines were tested for weed suppression against barnyardgrass. Rondo and its sister line yielded as well as the weed-suppressive indica standard (PI 312777), and approximately 50 % more than the least suppressive commercial cultivars in weedy plots (Gealy and Yan, 2012). Additionally, Rondo barnyardgrass biomass suppression was up to 1.5 times greater than commercially available U.S. cultivars (Gealy and Yan, 2012). Rondo combines high yield potential with rice blast resistance and weed suppressive ability, and is already being grown in commercial organic rice production in Texas (Gealy and Yan, 2012). No controlled bioassays have been conducted to measure the allelopathic potential of Rondo and its sister line. However, based on the allelopathic activity demonstrated by a number of other Asian indica lines (Dilday et al., 1994; Kim et al., 2005; Seal and Pratley, 2010), it is conceivable that allelopathy complements the effects of competitive traits in this cultivar.

Breeding Weed Suppressive Rice Cultivars in Asia Many of the same weed suppressive rice lines identified in the USDA rice breeding program in Arkansas are being used in rice breeding programs in Asia (Kong et al., 2011). Two particularly promising F₈ generation lines derived from crosses between local cultivars N9S and Huahui354 with PI 312777 were named, respectively, Huagan 1 and 3, and tested with their parents in yield trials overseeded with barnyardgrass (Kong et al., 2011). Although weed suppression by Huagan 3 is impacted by year to year variation and planting density, it was generally able to reduce barnyardgrass biomass by 80 % and total paddy weed biomass by 30 to 50 % compared to neighboring rice-free control plots. Huagan 3 was released as the first commercially acceptable weed suppressive cultivar in China (Kong et al., 2011). Kong et al. (2011) estimated that Huagan 3 was grown on over 10,000 ha in South China from 2009 to 2011.

Efforts to develop allelopathic rice cultivars have also been initiated by Korean breeding programs (Ma et al., 2006). F₄ and F₅ lines obtained through single seed descent from a cross between allelopathic, Kouketsumochi, and non-allelopathic but high yielding, Donginbyeon, cultivars were evaluated in the field for weed suppressive ability and screened for production of phenolic compounds. K21 was selected as the most promising line because it combined an inhibitory effect almost as strong as the allelopathic parent, with agronomic performance on par with the non-allelopathic parent (Ma et al., 2006). Lee et al. (2008) later confirmed the allelopathic activity of K21 with a bioassay that examined barnyardgrass seedling growth inhibition by rice root exudates.

Researchers in Cambodia have screened locally adapted germplasm for allelopathy and weed suppressive ability (Pheng et al., 2009a, b). ‘Relay seeding’ and washed sand bioassays were used to screen 359 Cambodian rice cultivars and global accessions (Pheng et al., 2009a). Approximately 4 % of accessions tested were allelopathic against awnless barnyardgrass. Pheng et al. (2009a) also measured the allelopathic potential of various lines against barnyardgrass, smallflower flat sedge, two-leaf fimbriatylis (*Fimbristylis miliacea*), water primrose (*Ludwigia octovalves*), and gooseweed (*Sphenoclea zeylanica*) in washed sand bioassays, and found that few accessions were allelopathic against multiple weed species. The weed suppressive effects of six Cambodian rice lines with allelopathic potential against barnyardgrass, smallflower flat sedge, and water primrose then were compared to the performance of allelopathic (TN-1) and non-allelopathic (ST-3) checks (Pheng et al., 2009b). The Cambodian lines out performed both allelopathic and non-allelopathic checks in weed suppression and grain yield in weedy plots. The observed differences in weed suppression may be due in part to competitive effects; the Cambodian lines were significantly taller (all over 100 cm) than Taichung Native 1 (55 cm) and ST-3 (91 cm) (Pheng et al., 2009b).

Breeding Weed Suppressive Rice in Africa A breeding program aimed at combining competitive traits from African rice (*O. glaberrima*) with yield alleles from *O. sativa* was initiated at the West African Rice Development Association (WARDA) (Fofana and Rauber, 2000; Olofsdotter et al., 2002). In a study evaluating the weed suppressive ability of *O. sativa* and *O. glaberrima* upland rice cultivars in low input agricultural systems in West Africa over two growing seasons, *O. glaberrima* accessions were consistently the best suppressors of weed biomass. Intra-specific variation in weed suppressive ability also was noted, where accession IG10 (*O. glaberrima*) suffered no yield losses in weedy conditions and suppressed weed biomass accumulation four times more effectively than *O. sativa* cultivars (Fofana and Rauber, 2000). A higher incidence of allelopathy was found

in *O. glaberrima* accessions than *O. sativa* accessions in a previous study (Fujii, 1992), so it is possible that competitive effects are complemented by the action of allelopathy in the field.

Incompatibility barriers prevented crosses between *O. sativa* and *O. glaberrima* in the past, but fertile interspecific progenies have been achieved through backcrossing and doubled haploid breeding (Jones et al., 1997). Interspecific hybrid lines yielded competitively with *O. sativa* cultivars in high input conditions and exhibited superior performance in low input conditions. Interspecific progeny also possess morphological traits generally associated with competitive ability, including droopy leaves during early growth stages and rapid vegetative growth early in the growing season (Jones et al., 1997).

Breeding Wheat for Improved Weed Suppression Breeding efforts targeted toward the improvement of weed suppressive ability in barley and wheat are still in the beginning stages compared to similar efforts in rice. Swedish breeding efforts at Svalöf Weibull (now Lantmännen Seed) and the Swedish University of Agricultural Sciences have made the most progress to date (Bertholdsson, 2007, 2010; Bertholdsson et al., 2012). Many other programs have evaluated barley (e.g., Christensen, 1995; O'Donovan et al., 2000; Watson et al., 2006; Paynter and Hills, 2009; Galon et al., 2011) and wheat (e.g., Balyan et al., 1991; Verschwele and Niemann, 1993; Blackshaw, 1994; Huel and Hucl, 1996; Lemerle et al., 1996, 2001a; Seavers and Wright, 1999; Acciaresi et al., 2001; Wicks et al., 2004; Vandeleur and Gill, 2004; Mason et al., 2008; Drews et al., 2009), accessions and cultivars for weed suppressive ability, but reports of their cultivar development activities are lacking in the literature.

Bertholdsson (2005) first assessed the role of competitive traits and allelopathy in determining weed interference outcomes for barley and spring wheat accessions in the field. Then, Mohan 73, a highly allelopathic Tunisian cultivar, was identified in a large bioassay screen of 813 spring wheat cultivars (Bertholdsson, 2010). Mohan 73 subsequently was crossed to an adapted but low allelopathy Swedish cultivar, Zebra. F₂ seedlings from the cross were evaluated for allelopathy by using the ‘equal compartment agar method.’ No improved transgressive segregates were identified. Strongly and weakly allelopathic F_{2,3} lines then were evaluated for agronomic performance in an unreplicated organic field trial (Bertholdsson, 2010). Three highly allelopathic lines, one low allelopathy line, and cultivar Zebra were chosen for further replicated tests (Bertholdsson, 2010). Mean early weed biomass was significantly lower in the highly allelopathic lines compared to the non-allelopathic parent and low allelopathy lines. Unfortunately, the high allelopathy lines were also significantly lower yielding than the low allelopathy lines (Bertholdsson, 2010). It is unclear whether the

low yields observed in high allelopathy lines were due to some physiological response caused by the action of allelopathy or by linkage drag from the poorly adapted allelopathic parent used in this cross.

Bertholdsson (2011) assessed the relative importance of allelopathy and competitive traits in determining the weed suppressive ability of winter wheat cultivars in Sweden. The range of early vigor and allelopathy accessible in global wheat germplasm is far lower than in other species such as rice (Olofsdotter et al., 2002), barley (Bertholdsson, 2005), and rye (Kruidhof et al., 2009). Therefore, Bertholdsson et al. (2012) evaluated translocations from *Triticum*, *Secale*, triticale (x *Triticosecale*), and wheat-rye substitution lines as possible sources of improved early vigor and allelopathy. No *Triticum* translocations were of particular interest, but potentially allelopathic triticale lines were identified. 1R and 2R wheat-rye substitution lines showed high allelopathic activity. In addition to accessing allelopathic germplasm from secondary and tertiary gene pools, researchers also should concentrate on improving competitive traits in wheat and barley. Given the time required to develop and release a successful cultivar, the release of a wheat cultivar with improved allelopathy or weed suppressive ability is likely still many years in the future.

Future Prospects

Researchers have suggested that breeding efforts for improved weed suppression should be postponed until our understanding of allelopathic phenomena is more complete (Olofsdotter et al., 2002), but annual grain cultivars are usually released at least 10 years after initial crosses are made. The first allelopathic rice lines were identified in 1985 (Dilday et al., 1991) and the first successful release of an allelopathic rice cultivar occurred only within the past 5 years (Kong et al., 2011). Given the extended timetable required for a successful cultivar release, breeders should begin to make crosses soon after promising weed suppressive lines are identified.

The morphological traits contributing to the competitive activity of genotypes and the role of allelopathy vary significantly depending on the crop species, environmental conditions, weed species of importance, and timing of the critical period for weed competition. Furthermore, local adaptation plays a major role in determining the yield potential and weed suppressive ability of grain cultivars (Cousens and Mokhtari, 1998; Olofsdotter et al., 2002; Wicks et al., 2004). Therefore, researchers in each region will need to conduct pilot trials to determine the traits that confer the most competitive advantage to crop cultivars and develop the most appropriate breeding schemes and objectives for their specific programs.

Weed suppressive cultivars must meet industry standards for yield, disease resistance, and a whole suite of other

characters (Gealy and Yan, 2012). Thus, breeding efforts for weed suppressive ability are more likely to release successful cultivars when weed suppression trials are integrated with larger breeding programs focused on increased productivity and a wide range of other locally important traits. In the USDA rice breeding program, the selection priorities in crosses between weed suppressive indica lines and adapted long-grain cultivars has been: high yield, followed by appropriate plant/grain characteristics (e.g., a lack of lodging and high milling yield), followed by weed suppression (Gealy et al., 2005a, b).

Breeders must judiciously decide where to utilize their limited time and resources. The relative importance of allelopathy and competitive traits may differ across species; hence, emphasis may be better placed in one area or another depending on the crop. Allelopathy explained only 0–21 % of the observed phenotypic variation in weed suppressive ability in wheat (Bertholdsson, 2005), as compared to 34 % in rice (Olofsdotter et al., 1999) and 7–58 % in barley (Bertholdsson, 2005). Researchers seeking to improve the weed interference potential of wheat cultivars in their region will, therefore, likely achieve the greatest results for resources expended by focusing on competitive traits.

Applications in Low Input and Organic Production Systems Weed suppressive crop plants are not likely to eradicate weeds as thoroughly as synthetic herbicides (Fitter, 2003; Gealy et al., 2003; Kong et al., 2011). Consequently, the applications of weed suppressive grain cultivars might be most important to developing world farmers and to the organic market. Cambodian researchers described major weed problems caused by erratic rainfall that prevented continuously flooding in rice crops (Pheng et al., 2009b). Herbicides were too costly for many Cambodian farmers to use, and hand weeding was the primary method for weed control in these agricultural systems (Pheng et al., 2009b). West African smallholder farmers also cited weed competition as the main limiting factor for upland rice yield, and noted that weed pressure was becoming more problematic as farmers increasingly moved from shifting cultivation systems to sedentary agriculture (Fofana and Rauber, 2000). Improved cultivars that yield consistently and suppress weeds are particularly valuable in such agricultural systems, as farmers do not require training or specialized equipment to benefit (Courtois and Olofsdotter, 1998). Locally adapted accessions were among the most weed suppressive material screened in both Africa and Cambodia (Fofana and Rauber, 2000; Pheng et al., 2009b). However, such landraces usually lack the yield potential of elite cultivars (Johnson et al., 1998). Therefore, the best course of action is to breed locally adapted germplasm with elite cultivars to combine yield potential with weed suppressive ability and adaptation to low input agriculture.

Weed suppressive grain cultivars also are appropriate for use in organic production systems, where herbicide use is not an accepted management practice. Organic grain production is increasing in Europe and North America, but few cultivars have been bred to meet the specific needs of organic producers (Wolfe et al., 2008). Weed pressure can create substantial economic losses for organic farmers; members of the North Carolina Organic Farm Advisory Board (OFAB) identified Italian ryegrass infestations as the most important agronomic limitation to organic wheat production in the southeastern United States and suggested that breeders select for lines that compete more effectively against weeds (Reberg-Horton pers. comm.). Successful cultivars targeted toward the organic market will have to combine weed suppressive ability with high yield potential, disease resistance, and quality traits (Gealy and Yan 2012).

Conclusions Weed suppressive rice cultivars are now commercially available in the U.S. (Gealy and Yan, 2012) and China (Kong et al., 2011), with more promising lines currently being evaluated in advanced trials (Gealy et al., 2010). Rice research on weed suppressive ability has been successful because of the sustained breeding efforts conducted over the past three decades at the Dale Bumpers Rice Research and Extension Center, IRRI, and collaborating institutions. Collaboration between agronomists, breeders, and biochemists, also has allowed for a more complete understanding of allelopathy and competition in rice. Furthermore, researchers around the world have shared information and germplasm, allowing each program to cross the most promising global accessions with their own locally adapted material. The groundwork has been laid for the development of weed suppressive wheat and barley cultivars in Sweden (Bertholdsson, 2005, 2011; Bertholdsson et al., 2012). Meanwhile, many other research teams have evaluated locally adapted germplasm and global wheat accessions for competitive traits and allelopathy. Provided that there is successful collaboration among these programs and sustained funding and research efforts, weed suppressive wheat and barley cultivars could be released within the next decade. Breeding efforts conducted in wheat, barley, and rice also may be informative to researchers embarking on new projects targeted toward the development of weed suppressive grain cultivars in other crop species.

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