Agriculture, Ecosystems and Environment 208 (2015) 29–36

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Review

Moving beyond resistance management toward an expanded role for seed mixtures in agriculture

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ARTICLE INFO

Article history:
Received 8 August 2014
Received in revised form 13 April 2015
Accepted 17 April 2015
Available online 1 May 2015

Keywords:
Bt
Cultivar mixture
Intraspecific diversity
Seed mixture
Sustainable

ABSTRACT

Insect resistance management for *Bt* traits in corn has recently moved toward refuge-in-the-bag, which consists of simple cultivar mixtures of susceptible and resistant hybrids. The purpose of these seed mixtures has thus far been solely to maintain susceptible pest insects, which will help prevent the development of resistance and preserve utility of the technology. It appears that this narrow focus on resistance management overlooks broader production benefits that may be achieved by planting genotypically diverse cultivar mixtures. While not yet widely employed in modern agriculture, cultivar mixtures have been successfully used for disease management, demonstrating that the strategy is logistically feasible for intensified agriculture. Evidence from both natural and agricultural systems demonstrates that more genotypically diverse plantings can increase yield or productivity through a variety of mechanisms. These effects are in part attributable to improved response to both abiotic and biotic stressors, such as drought, temperature stress, competitors, herbivores, and disease. Similar to transgenic traits, cultivar mixtures also hold promise for resistance management for traditionally bred, or native, traits.

Contents

1. Introduction

Across the U.S., many farmers are now growing simple "cultivar mixtures" when they plant their transgenic, insect-resistant corn containing proteins from the soil bacterium *Bacillus thuringiensis* (*Bt*). Cultivar mixtures are blends of crop varieties that are agronomically similar enough to be grown together, but possess key phenotypic differences, such as differences in disease or insect resistance (Wolfe, 1985). Farmers in the U.S. are planting corn seed that is a mixture of *Bt* and non-*Bt* hybrids, commonly known as "refuge-in-the-bag" (RIB). The purpose of these seed mixtures has thus far been to prevent pest insects from developing resistance

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http://dx.doi.org/10.1016/j.agee.2015.04.019

against *Bt* toxins by using non-*Bt* seeds as a refuge. This is a change from the previous sole reliance on non-*Bt* refuges that are spatially separate from *Bt* plants. By mixing different types of seeds together to create a ready-to-plant integrated refuge, seed companies have generated simple cultivar mixtures. These are recognized as effective tools for managing plants pathogens to increase yield (Mundt, 2002; Wolfe, 1985). Current corn seed mixtures intentionally contain limited diversity relative to typical cultivar mixtures (Mundt, 2002), but it may be possible for seed companies to develop cultivar mixtures that capitalize on other ecological benefits of intraspecific diversity (aka genotypic diversity), such as managing pathogens, herbivores, and abiotic stressors (Hajjar et al., 2008; Tooker and Frank, 2012).

The objective of this paper is to link the current insect resistance management (IRM) strategy of seed mixtures to the broader discussion on the role of genotypic diversity in ecosystems. Subsistence farmers around the world often grow cultivar mixtures for pest management, risk avoidance, and overall yield benefits (Smithson and Lenné, 1996), but in conventional agriculture, cultivar mixtures remain poorly explored. We seek to bridge the gap between reviews that have focused on benefits of cultivar mixtures for specific goals (e.g., disease or insect management, insect resistance management; Mundt, 2002; Onstad et al., 2011; Tooker and Frank, 2012) and current use of RIB seed mixtures to emphasize potential benefits of cultivar mixtures. First, we will highlight empirical evidence from natural and agricultural systems to illustrate some of the ecological benefits that may be derived from cultivar mixtures. We will then describe the current rise of cultivar mixtures for managing resistance to transgenic *Bt* traits to contextualize how cultivar mixtures are currently employed in *Bt* crops. We will also describe the role cultivar mixtures can serve for managing resistance for native, or non-transgenic, traits. Finally, we will consider a broader future role for cultivar mixtures in pest management and agriculture, with an emphasis on their use in intensified production of annual crops and primarily in the U.S., though the discussion is pertinent to many types of agriculture.

2. Genotypic diversity in ecosystems and ecological benefits

Typical modern agricultural fields are planted with a single variety of a single crop species and therefore tend to have limited species and genetic diversity (Bonneuil et al., 2012). A diverse body of research from both crop and natural systems, however, provides evidence that increasing crop genotypic diversity via cultivar mixtures may help to improve plant productivity by buffering agroecosystems against a range of stressors. Much of this evidence comes from non-crop systems, but the underlying ecological principles and mechanisms are likely to be similar in both types of systems.

Crop systems differ from natural systems in ways key to understanding the potential for applying information on within-species diversity from natural systems to crop fields. Natural communities self-assemble and usually persist across multiple seasons and generations, allowing changes in diversity through natural selection to accumulate with time (Bell, 1991; Stuefer et al., 2009). Growers of annual species (e.g., corn, wheat) largely determine the composition of their crop when they plant their fields, setting levels of genotypic diversity at the beginning of the season each year and permitting manipulation of genotypic diversity for specific production goals. If growers do not save and replant seed from the mixture, selection generally does not change the relative abundance of genotypes, unless an extreme event occurs (e.g., weather, pests). Some forage, biofuel (e.g., switchgrass, willow), or fruit systems are perennial, and in these fields the relative abundance of genotypes can shift.

2.1. Yield

Because yield is one of the key factors influencing farmer adoption of a new practice, it is promising that higher levels of genotypic diversity can increase plant productivity or reproductive output (i.e., yield) in a diverse array of crop and non-crop plant species (Cook-Patton et al., 2011; Crutsinger et al., 2006; Johnson et al., 2006; Kiær et al., 2009; Smithson and Lenné, 1996). For non-crop plant species, increases in plant productivity or reproductive output from higher intraspecific diversity (measured by above-ground biomass or seed production) have varied from 3 to 35% (Cook-Patton et al., 2011; Crutsinger et al., 2006; Johnson et al., 2006). This range is somewhat similar to yield increases for cultivar mixtures of crop plants, which tend to be around 5–10%, but have reached 30% for mixtures that effectively suppress disease outbreaks (Smithson and Lenné, 1996; Wolfe, 1985). Notably, these increases are comparable to increases in productivity and reproductive fitness that have been observed from increasing interspecific diversity (Cook-Patton et al., 2011; Crutsinger et al., 2006).

Intraspecific diversity can increase productivity relative to monocultures when genotypes benefit from presence of another genotype and/or divide up the available niche space and resources (complementarity), or when genotypic diversity leads to a higher probability of including in the mixture a productive or well-adapted genotype (sampling effect; Hughes et al., 2008; Loreau and Hector, 2001). One argument against cultivar mixtures has been growers could just plant a well-adapted genotype rather than complicate matters with a mixture, but it should be recognized that identifying the variety that will do well in the coming growing season can be challenging, and a mixture increases the chances of having that variety in the field. In crop fields, effects driven by complementarity, or instances in which certain genotypes facilitate or support other genotypes, are likely more influential than selection effects because the frequency of genotypes tends to stay consistent. Moreover, recent research has found plants can recognize relatedness of neighbors of the same species and then express different phenotypes and strategies of growth or biomass allocation when they are surrounded by kin or non-kin plants; these phenotypes have potential to produce cascading effects that influence herbivore populations (Dudley and File, 2007; File et al., 2012). Changes in phenotypic expression other than productivity and yield, such as defensive chemistry or drought resistance, affect responses of the plant community to its abiotic and biotic environment and could alter relationships between diversity and productivity (Agrawal et al., 2006).

2.2. Abiotic stressors

Abiotic stressors, including extremes in soil pH, temperature, salinity, and water availability, constrain productivity in many ecological systems, including agricultural fields, and plantings of genotypically diverse mixtures tend to be more resilient to abiotic stress than monocultures (Ehlers et al., 2008; Peltonen-Sainio and Karjalainen, 1991). In natural systems for example, increased genotypic diversity in eelgrass stands enhanced biomass production and shoot density following extreme, naturally occurring heat stress, in part due to niche partitioning or complementarity among genotypes (Reusch et al., 2005). In the same system, genetic diversity improved stem density during winter when stands were subjected to a variety of abiotic stressors (e.g., lower light, desiccation, and lower salinity; Hughes and Stachowicz, 2009).

Similar to its role in natural systems, genotypic diversity can also buffer agricultural fields and crop yield against abiotic stressors by both maintaining and reducing variability in yields (Dawson and Goldringer, 2012). Yield compensation occurs in cultivar mixtures when individual genotypes respond variably to