Agriculture, Ecosystems and Environment 127 (2008) 1–6

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Review

Crop ferality: Implications for novel trait confinement

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ARTICLE INFO

Article history:
Received 11 September 2007
Received in revised form 6 March 2008
Accepted 18 March 2008
Available online 19 May 2008

Keywords:
Crop ferality
GM crops
Gene flow
Trait confinement
Co-existence

ABSTRACT

Ferality is observed in many crop species wherein individuals of the cultivated crop reproduce successfully and establish a self-perpetuating population in natural or semi-natural habitats. Feral populations can evolve to differ from their parent populations and lose traits associated with domestication including for example, a lack of seed dormancy. Hybridization between wild and cultivated forms of cropped species may facilitate ferality. If GM plants become feral, they can establish populations in natural and semi-natural environments and act as both a source and sink for novel traits. The presence of novel traits may facilitate the persistence of feral populations if the novel trait confers a selective advantage (e.g. drought tolerance, salinity tolerance, pest and disease resistance), but there is no evidence yet that transgenesis *per se* facilitates ferality. In some cases and in some jurisdictions, the introduction of GM crops will require assurances of effective segregation and novel trait confinement. The existence of feral crop populations can make novel trait confinement more difficult. Monitoring and management of feral populations will be required for effective novel trait confinement.

Contents

1. Introduction

The introduction of new GM crops becomes a greater concern as traits that are ever more extraordinary are introduced into crop plants, in particular, pharmaceutical and industrial traits. Most risks associated with the release of crops with such extraordinary traits are related to trait movement (Marvier and Van Acker, 2005). Trait confinement protocols will be required for the commercialization of some GM crops (Demeke et al., 2006) and effective trait confinement is necessary to facilitate the co-existence between GM and non-GM crops (Damgaard and Kjellsson, 2005; Jank et al., 2006). In this respect, feral populations of cultivated species can play an important role in novel trait escape and movement (Rabbani et al., 1998; Berville et al., 2005a; Snow and Campbell, 2005; Devaux et al., 2007). Occurrence of feral populations has been reported for a number of crop species (Crawley and Brown, 1995; Baki et al., 2000; Ellstrand, 2003; Stewart et al., 2003; Burger et al., 2006; Bagavathiannan et al., 2006; cf. Table 1) and the occurrence of GM crop volunteers has been widely studied (Tølstrup et al., 2003). However, the occurrence of cultivated

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0167-8809/$ – see front matter
doi:10.1016/j.agee.2008.03.009

Table 1
Summary of reports on crop species ferality or potential ferality

Species	Probable origins	Potential regions	References
Oilseed rape	Seed spill during transportation, farm machineries, cross between *B. napus* and *B. campestris*	Europe (UK, France, Denmark), USA, Canada	Rich (1991), Crawley et al. (1993), Crawley and Brown (1995), Wilkinson et al. (1995), Wilkinson et al. (2000), Gray and Raybould (1998), Pessel et al. (2001), Hails et al. (2002), Bond et al. (2004), Cresswell and Osborne (2004), Claessen et al. (2005a), Claessen et al. (2005b), Garnier et al. (2006)
Radish	Cross between cultivated radish (*R. sativum*) and weedy relative (*R. raphanistrum*)	USA, Japan, Pakistan	Rabbani et al. (1998), Snow et al. (2001), Nature Conservancy (2005), Snow and Campbell (2005), Hedge et al. (2006)
Rye	Cross between cultivated (*S. cereale*) and mountain rye (*S. strictum*), dedomestication	USA	Stump and Westra (2000), Berville et al. (2005b), Burger and Ellstrand (2005), WCO (2005), Burger et al. (2006), White et al. (2006)
Cotton	Seed escape, cross between cultivated (*G. hirsutum*) and pima cotton (*G. barbadense*)	USA (Florida, Hawaii), U.S. Virgin Islands, Puerto Rico	Ellstrand et al. (1999), USEPA (2001)
Alfalfa	Seed spill during transportation, farm machineries, anthropogenic factors	USA, Canada	Fitzpatrick et al. (2003), Bagavathiannan et al. (2006), Bagavathiannan et al. (2007)
Sugar beet	Cross between cultivated (*B. vulgaris* ssp. *vulgaris*) and wild beets (*B. vulgaris* ssp. *maritima*)	Europe (France, Belgium, Germany), USA (California)	Bartsch et al. (1996), Desplanque et al. (1999), Ellstrand (2003), Sukopp et al. (2005)
Sunflower	Seed escape, cross between *H. annuus* and *H. tuberosus*	USA, Europe	Faure et al. (2002), Massinga et al. (2003), Stewart et al. (2003), Berville et al. (2005a), Massinga et al. (2005)
Wheat	Seed escape, dedomestication	USA, Canada, Europe, Tibet	Chen et al. (1998), Chen et al. (1999), Sun et al. (1998), Stewart et al. (2003)
Sorghum	Seed escape, dedomestication, cross between *S. bicolor* and *S. halepense* or *S. sudanense*	USA, Africa	Arriola and Ellstrand (1996), Arriola and Ellstrand (1997), Stewart et al. (2003), Ejeta and Grenier (2005)
Ornamentals	Exotic introduction, dedomestication	USA, Europe, Australia	Levin (2001), Stewart (2004), Kowarik (2005), AIPC (2007)
Meadow fescue	Seed escape	Norway, Sweden	Rognli et al. (2000)
Rice	Dedomestication	South East Asia, China, USA	Baki et al. (2000), Lu and Snow (2005), Valverde (2005), Vidotto and Ferrero (2005)
Vigna group (cowpea, rice bean, azuki bean)	Seed escape, cross with wild relatives	Asia	Berville et al. (2005b)
Safflower	Seed escape	USA, Canada, Mediterranean	Berville et al. (2005b)

species as feral populations has been studied to a limited extent, particularly in the context of novel trait confinement (Gressel, 2005a; Garnier et al., 2006; Devaux et al., 2007) yet there is an increasing interest in the nature of feral populations of cropped species (Ramsay et al., 2003; Cresswell and Osborne, 2004; Massinga et al., 2005; Garnier et al., 2006). The objective of this review is to provide a background on crop ferality, the nature of feral populations, the role of GM in ferality and insight into the problems associated with the occurrence of feral crops with respect to novel trait confinement.

2. Definitions

Gressel (2005b) defined feral plants as plants derived fully or in part from crop plants that have become partially or fully dedomesticated. However, a cultivated crop species that has escaped and is growing in an unmanaged environment with a self-perpetuating population could still be considered feral even if it retains all of its original traits. The important characteristic feature of feral crop populations is that they are able to successfully reproduce without management intervention (White et al., 2006). Although there is a clear distinction between volunteer and feral crop populations, the terms are not used consistently. Volunteers are derived from seeds that the crop has released before and during harvest (Gressel, 2005b). Warwick and Stewart (2005) defined volunteers as “crop plants that grow in the same field in subsequent crops or years from a seedbank formed from seed that either shattered from the crop prior to or as a result of harvesting operations or from originally sown seed that did not germinate immediately after sowing”. Gressel (2005b) suggested that crop volunteers could become feral within cultivated fields if they self-perpetuate but a more strict definition makes clear that feral populations exist in non-cropped areas. Claessen et al. (2005a) and Garnier et al. (2006), categorized ferals as populations outside of an arable field and volunteers as populations inside an arable field. Likewise, Devaux et al. (2007) described volunteers as plants from previously grown cultivars in fields and ferals as plants that are widespread in field verges or roadsides. Volunteers of most crop species rarely persist for more than one or two seasons. However, volunteers existing on field margins may contribute founding seeds for feral populations. One might term persistent volunteers as ‘weedy volunteers’ and volunteers that are found outside of cultivated fields, but are unable to sustain a population over time as ‘escaped crops’. In this review we will assume that volunteers exist in managed or cultivated environments while ferals exist in unmanaged natural and semi-natural habitats. A practical definition of ferality, therefore, is where individuals of a cultivated crop escape a managed area, survive, reproduce successfully and establish a self-perpetuating population in either a natural or semi-natural habitat.

3. The establishment of feral populations

Knowing how feral populations establish and evolve is fundamental to understanding ferality. Generally, the occurrence of feral forms of cultivated crop plants is initiated by the dispersal of seed from cultivated fields to adjacent unmanaged ecosystems. Seed dispersal could be facilitated by farm machinery (Crawley and Brown, 1995), seed spill during transport (Crawley and Brown, 1995; Gray and Raybould, 1998; Senior and Dale, 2002; Claessen et al., 2005a; Yoshimura et al., 2006), dispersal by vehicles (Garnier and Lecomte, 2006) and also by birds, rodents and other seed