Ecological Modelling 276 (2014) 85–94

Contents lists available at ScienceDirect

Ecological Modelling

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

A stochastic cellular model with uncertainty analysis to assess the risk of transgene invasion after crop-wild hybridization: Oilseed rape and wild radish as a case study

Aurelie Garnier[a], Henri Darmency[b], Yann Tricault[b,1], Anne-Marie Chèvre[c], Jane Lecomte[a,*]

[a] Univ Paris-Sud, CNRS, AgroParisTech, UMR 8079 Ecologie Systématique et Evolution, Orsay 91405, France
[b] INRA, UMR1347 Agroécologie, Institut National de la Recherche Agronomique, 17 rue Sully, Dijon BP 86510, 21065, France
[c] INRA, UMR1349 IGEPP, F-35653 Le Rheu Cedex, France

ARTICLE INFO

Article history:
Received 7 September 2012
Received in revised form
20 December 2013
Accepted 7 January 2014
Available online 4 February 2014

Keywords:
Elasticity analysis
Transgene flow
Human-mediated seed dispersal
Invasion
Risk assessment
Stage-structured population dynamics

ABSTRACT

Crop-to-wild transgene flow is a critical aspect of the environmental risks associated to the introduction of genetically modified (GM) crops because the integration of an advantageous transgene could make the recipient population of wild species become invasive. This risk relies on three successive steps: (1) the initial GM crop-wild hybridization event, (2) the transmission of the transgene in the successive (backcross) hybrids generations and (3) the spread of the GM hybrid plants via pollen and seed dispersal. Using simulation models is necessary to account for the probabilities associated to all these events in order to make quantitative predictions of the risk of invasion by GM hybrids. We develop a simulation model to predict the fate of an advantageous transgene in a population of a wild relative species, following hybridization with a GM crop. We first present the generic model structure, with its three main components: stage-structure (developmental stages and hybrid classes), spatial realism, and stochasticity (demographic, genetic and dispersal). We show how a preliminary elasticity analysis can be performed to guide the parameterization of an uncertainty analysis by focusing on the most influencing parameters. We then use herbicide tolerant GM oilseed rape and its wild relative wild radish as an application of the simulation model. Despite the large uncertainty on some input parameters, simulations showed that invasion by the transgene was quasi-impossible within decaying wild radish populations whereas it was quasi-certain within viable populations. More generally, the modeling framework developed here provides a generic structure that can be applied to other wild and crop species. Our study underlined that uncertainty analyses are crucial in risk assessment because they permit to translate parameter uncertainty into uncertainty of model predictions.

1. Introduction

Assessing the risks of transgene escape in the environment is crucial to guide decision-makers about the deployment of genetically modified (GM) cultivars into a new region and to design crop systems that limit unintended transgene flow (Ellstrand et al., 1999). Interspecific hybridization between GM crop species and their wild relatives is a major concern because it means that the transgene can no longer be controlled. Crop-wild hybrids may either exhibit enhanced fitness if the transgene confers a selective advantage (e.g. Snow et al. (2003) for *Bt* resistance to insects in wild sunflowers; Fuchs et al. (2004) for hybrids of wild and virus-resistant transgenic squash), or reduced fitness if the expression of the transgene alters their life-cycle (e.g. Linder and Smidt (1995) for oil-modification transgenes and consequences in seed dormancy and survival).

The invasion of a population of a wild relative species by a transgene requires several steps: the initial crop-wild hybridization event, the production of viable and fertile F1 hybrids, the successful transmission of the transgene through subsequent hybrid generations (F2, backcross generations: BC1, BC2,. . .,BC*n*) and the spatial spread (through pollen or seeds) of advanced

---

* Corresponding author at: Univ Paris-Sud, Laboratoire Ecologie Systématique et Evolution, UMR8079, Orsay F-91405, France. Tel.: +33 1 69 15 76 57; fax: +331 69 15 46 97.

E-mail addresses: au.garnier@gmail.com (A. Garnier), henri.darmency@dijon.inra.fr (H. Darmency), Yann.Tricault@agrocampus-ouest.fr (Y. Tricault), anne-marie.chevre@rennes.inra.fr (A.-M. Chèvre), jane.lecomte@u-psud.fr (J. Lecomte).

[1] Present addresses: AGROCAMPUS OUEST, UMR1349 IGEPP, F-49000 Angers, France/LUNAM Université, France.

0304-3800/$ – see front matter © 2014 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.ecolmodel.2014.01.004

generations of hybrids carrying the transgene. The integration of the transgene in the wild relative species can be either an introgression sensu stricto, i.e. the stable incorporation of the transgene into the genome of the wild relative species (Stewart et al., 2003), or the simple transmission of an additional (or fraction of) crop chromosome that carries the transgene (e.g. Al-Mouemar and Darmency (2004) for wild radish–oilseed rape hybrids).

Integration/introgression of crop transgenes into wild relatives is expected to occur for many crop species, including wheat, sugar beet, oilseed rape, alfalfa, sunflower and sorghum (see the review of Stewart et al. (2003) and Andersson and Vicente (2009)) and for some tree species (van Frankenhuyzen and Beardmore, 2004). Crop-to-wild transgene flow could be especially noxious when the species of wild relative is a weedy species: an advantageous transgene could make weed relatives even more invasive and difficult to control, thus resulting in agronomical issues (Raybould and Gray, 1994; Stewart et al., 2003; Pilson and Prendeville, 2004; Chapman and Burke, 2006).

Models are efficient tools to predict the fate of a transgene in a population of a wild relative species because they can explore the relevant temporal (decades) and spatial (hectares) scales. We chose to develop a simulation model because it permitted to relax some simplifying hypotheses of analytical approaches (e.g. a constant or infinite population size in Haygood et al. (2003) and Huxel (1999) respectively; non-overlapping generations in Huxel (1999), Haygood et al. (2003) and Thompson et al. (2003)). It thus allowed us to include a higher level of realism in plant-life cycle, genetic aspects and spatial aspects. Three components were essential to account for by the model, in order to assess the risks of invasion of a population of a wild relative species by a crop transgene. First, the stage-structure permits to distinguish the successive developmental stages (seeds, seedlings, mature plants – Caswell, 2001) and crop-wild hybrid generations (F1, F2, BC1,. . .,BC*n* – Hooftman et al., 2007). Secondly, introducing different types of stochasticity permits to account both for the impact of potentially low plant numbers on demographic transitions (demographic stochasticity – Caswell, 2001) and to correctly model low probability events that govern the fate of the transgene in the population of the wild relative species, such as initial crop-wild hybridization, transgene transmission rate to progeny (genetic stochasticity, i.e. genetic drift), or long distance seed dispersal (stochasticity in dispersal). Third, an appropriate spatial representation allows adequate modeling of spatial heterogeneities and seed/pollen dispersal through dispersal kernels (modeling the proportion of seeds/pollen dispersing at each distance – Clark, 1998; Chesson and Lee, 2005).

Some simulation models, that include high levels of spatial and demographic realism, have been already developed to predict the escape of transgenes from cultivated crops or GM trees, but most are monospecific, such as the deterministic modeling platform GeneSys Colbach et al. (2001a,b) for oilseed rape; Sester et al. (2008) for sugar beet and weed beet – purely deterministic models) and the stochastic models AMELIE (for annuals or perennials – Kuparinen and Schurr, 2007, 2008) and STEVE (for trees – DiFazio, 2002; Slavov et al., 2004). The spatial model GeneTraMP (Middelhoff et al., 2011) is plurispecific but does not consider explicitly the successive crop-wild hybrid generations. Conversely, some other models describe explicitly the different interspecific hybrids classes, but do not encompass a spatial component (e.g. Ferdy and Austerlitz (2002) for a theoretical model of introgression in plants; Hooftman et al. (2007) for *Lactuca*) or include a set of discrete patches but with no explicit spatial arrangement and no dispersal kernel for seed dispersal (Wolf et al., 2001).

We develop here a stage-structured stochastic 2D cellular model to predict the fate of a crop transgene in a population of a wild relative species at the scale of a single cultivated field, when crop-wild hybridization occurs. The generic structure of the model, including the demographic, genetic and spatial components, is first presented in a general point of view (Section 2). We then present an elasticity analysis as a preliminary step of a parameter uncertainty analysis (Section 3): the uncertainty of the most influencing parameters, identified by the elasticity analysis, is then modeled using probability distributions. The uncertainty analysis then permits to construct confidence intervals for output variables (Buckley et al., 2005). In Section 4, we apply the simulation model to the case of oilseed rape (*Brassica napus* L.) and its wild relative wild radish (*Raphanus raphanistrum* L.). We finally discuss on the potential applications of the model to other crop-wild plant species and we address the issue of high parameter uncertainty that may lead to unpredictability.

2. Generic model structure

2.1. Demographic component: life-cycle of the wild relative species

The model computes on an annual basis the number of plants (which can be thereafter translated into plant density, knowing the corresponding surface area) in the successive developmental stages of the life-cycle of the wild relative. This life-cycle can be annual, biennial or perennial, with a seedbank or not, depending on the species. For example, the developmental stages for an annual life-cycle with a soil seedbank are (Fig. 1): seeds in the seedbank (**S**), seedlings (**R**) emerged from seedbank seeds, mature plants (**FR**) and new seeds (**S_0**) produced by mature plants. The demographic parameters (Fig. 1) either correspond to transition probabilities in the life-cycle (emergence rate (g), survival rates of seeds in the seedbank (s_s), of seedlings up to plant maturity (s) and of new seeds after seed predation (s_P)) or to per-capita seed production of mature plants (f). Parameters of the wild species life-cycle depend notably on the type of crop in which the wild relative grows (see Section

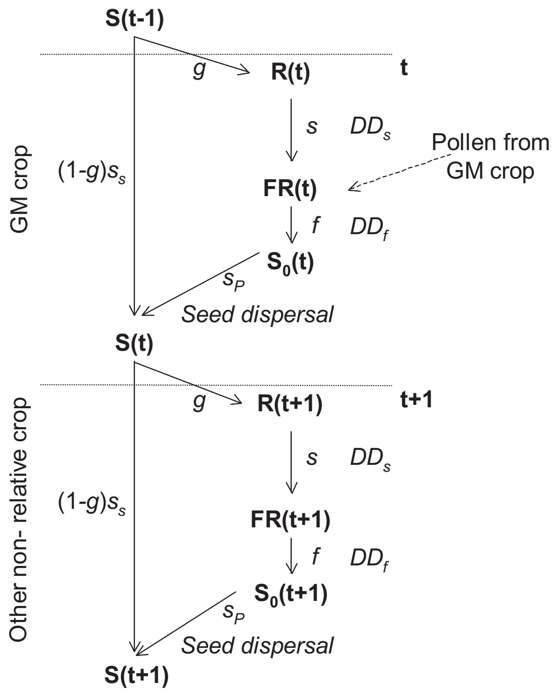

Fig. 1. Example of life-cycle for an annual (i.e. one generation per year **t**) wild relative species with a soil seedbank. Developmental stages are: seeds in the seedbank (**S**), seedlings (**R**), mature plants (**FR**), new seeds produced by mature plants (**S_0**). See text (Section 2.1) and Table A1 for definitions of the demographic parameters. Demographic parameters of the wild relative species can depend on the crop in which the wild plants grow (see Section 3.1.1).