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Contribution of groundkeepers vs. weed beet to gene escape from sugar beet (*Beta vulgaris* spp.). Consequences for growing genetically-modified sugar beet – A modelling approach

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ABSTRACT

Weed beet cannot be controlled by herbicides in sugar beet (except via height-selective applicators) as it is a crop relative, descending from accidentally flowering sugar beet (*Beta vulgaris*) crop plants either because of vernalization during cold springs, or presence of a dominant bolting allele in sugar beet seed lots due to cross-pollination by annual wild beet (*B. vulgaris* ssp. *maritima*) in seed production areas. A second, minor source of weed beet are crop roots lost during harvest. These roots ("groundkeepers") can reproduce in the year after sugar beet and potentially contribute to weed beet dynamics and gene flow. Bolting, flowering and seed production timing and potential of groundkeepers were measured in field experiments. Bolting and flowering were faster in groundkeepers vs. weed beet; flower and seed production was lower in groundkeepers but the latter were less sensitive to competitive crops. The measured parameters were used to introduce a ground-keeper life-cycle into the GeneSys-Beet model which quantifies the effects of cropping systems on weed beet in landscapes. Simulations over several years showed weed beet dynamics to be more sensitive to groundkeeper parameter values than to root loss at sugar beet harvest. Groundkeepers were identified as a key source of weed beet populations and of gene escape from novel sugar beet varieties (e.g. genetically-modified herbicide-tolerant varieties) in the absence of crop bolters. The control of the latter, either by manual weeding or by genetic improvement of sugar beet varieties, was shown to be essential for controlling weed beet populations and avoid the advent of herbicide-tolerant weed beet.

1. Introduction

Weed beet is an annual weedy form of the genus *Beta*, i.e. *Beta vulgaris* ssp. *vulgaris* (Hornsey and Arnold, 1979), a frequent and harmful weed in sugar beet (*B. vulgaris*) fields (Sweet et al., 2004). Because of its genetic proximity to sugar beet, there are no herbicides available for selectively destroying weed beets in conventional sugar beet crops, except via height-selective herbicide applicators aiming at tall vs. small plants. Weed beet management mainly relies on stale seed bed techniques (i.e. summer tillage emptying the weed seed bank by stimulating seed germination), interrow hoeing and manual weeding of bolters in sugar beet (i.e. beet plants with flowering and seed-producing stems). Another option is stimulating weed beet emergence in other crops of the rotation where herbicides against weed beet are available though the number of herbicides is steadily decreasing because of regulatory measures (e.g. the EU directive REACH, http://ec.europa.eu/environment/chemicals/reach/reach_intro.htm). The advent of genetically modified (GM) herbicide-tolerant (HT) sugar beet offers a new tool to manage weed beet (Richard-Molard et al., 1996; May, 2003). Even though the biannual sugar beet does usually not produce seeds in root-production areas, it is likely that the herbicide-tolerance gene could be transmitted from the crop to weed beet (Desplanque et al., 2002; Darmency et al., 2007), resulting in the advent of HT weed beet, thus cancelling one of the advantages of the GMHT sugar beet.

Indeed, weed beet is the progeny of sugar beet, descending mainly from accidentally flowering sugar crop plants, either because of vernalization during cold springs, or presence of a dominant bolting allele in sugar beet seed lots due to cross-pollination by annual wild beet (*B. vulgaris* ssp. *maritima*) in seed production areas (Boudry et al., 1993; Desplanque et al., 1999). An additional source of weed beet are groundkeepers, i.e. plants arising from roots left in the field after harvest, in the crop following sugar beet (Pohl-Orf et al., 1999). Whereas plant recruitment from seed banks and

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their subsequent reproduction has already been studied in several environments (Gunn and Dunkerton, 1981; Longden, 1993; Sester et al., 2004, 2006b), little is known about the growth and development of groundkeepers in crops following sugar beet as well as their contribution to weed beet dynamics and gene flow.

The objective of the present paper thus was to study flowering progress and seed production of groundkeepers in crops after sugar beet and to compare them to the behaviour of weed beet. In addition, the measured life-cycle parameters were introduced into a weed beet dynamics model to evaluate the contribution of groundkeepers to the advent and dynamics of weed beet population in time as well as their importance for gene escape from sugar beet crops in landscapes. The model chosen for this purpose was GeneSys-Beet model as the only model to day which quantifies the effect of cropping systems on weed beet dynamics and gene flow over time in landscapes (Sester et al., 2007, 2008).

2. Material and methods

2.1. The GeneSys simulation model

The GeneSys-Beet model is described in detail by Sester et al. (2007, 2008). The initial version was developed to assess accidental gene flow from sugar beet crops to weed beet populations, via pollen flow and seed production by accidentally bolting crop plants (i.e. growing a reproductive stem with flowers and viable seeds). Only the main points of the initial version will be presented here before describing the new submodel for growth and development of groundkeepers in the crop following sugar beet.

2.1.1. Input variables

The model uses the following input variables:

- the regional field plan consisting of all cultivated fields, each represented by the coordinates of its summits.
- the crop grown each cropping year in each simulated field, choosing between sugar beet, winter cereals, spring cereals, maize, pea and three types of non-arable cropping (defined subsequently in this paper as set-aside), i.e. sown (with an annual forage species such as clover), unsown (1-year fallow) and perennial (usually a pasture).
- the management techniques for each crop, i.e. tillage, sowing and harvesting dates, herbicides, mechanical weeding and cutting. Manual bolter-weeding (hand-pulling) is only applied in sugar beet.
- the daily weather data over the simulated period consisting of rainfall, mean, minimum and maximum temperatures. These input variables are also used to predict another kind of input variables, i.e. mean soil temperatures and water potential in successive 1-cm-thick soil layers from 0 to 30 cm depth (the maximal depth of tillage operations). These predictions are carried out with a submodel from the crop simulation model STICS (Brisson et al., 1998) recently linked to GeneSys.
- the initial seed bank of the field, with seed densities in each soil layer, distinguishing the seeds shed during the latest seed rain (hence 'young' seeds) from older seeds as well as seeds previously exposed to light while imbibed from unexposed seeds because they show different dormancy patterns (Sester et al., 2006b).

2.1.2. The life-cycle of sugar beet and weed beet in the initial GeneSys version

The initial GeneSys version considers three kinds of life-cycles. The sugar beet life-cycle starts with the sowing of the seeds and ends at the first year of the biannual life-cycle of the species, when the plants are harvested while still being at the rosette stage (Fig. 1A). If the sown seed lot is contaminated by annual hybrid seeds or if the plants are vernalized by late frost, sugar beet plants bolt during the first year of their life-cycle and can produce seeds (Fig. 1B). These then lead to the creation of a weed beet seed bank and the third kind of life-cycle consisting of only annual plants, either because of the annuality gene or because of vernalization of seeds in the seed bank (Fig. 1C).

These life-cycles co-exist in sugar beet crops whereas in other crops, only the weed beet life-cycle is simulated. The model operates on a daily time-step with life-stage densities (number of individuals m^{-2}) as state variables. Transitions between successive life-stages are driven by air temperature, soil temperature and moisture, with parameter values specific to the different types of seeds (dormant vs. non-dormant, young vs. old). Management techniques may both trigger developmental processes (e.g. germination flush after tillage) and change the vertical distribution of seeds in the soil (e.g. mouldboard ploughing) or cause mortality at stage-specific rates. Weed beet survival and reproduction are reduced by plant competition at crop-specific rates. The main output variables are, for each simulated year, the number of emerged weed beet seedlings, bolters, and seed bank left after harvest.

2.1.3. Integrating a life-cycle for groundkeepers

Here, a fourth life-cycle was added for crops following sugar beet, starting with unharvested roots that survive tillage and bolt during the second year of the biannual species life-cycle (Fig. 1D). These roots are vernalized during the winter following the sugar beet harvest and then bolt and reproduce in the next crop. The newly produced seeds are again added to the weed beet seed bank, and the plants originating from these seeds then behave as weed beets (i.e. life-cycle of Fig. 1C). This additional life-cycle requires an extra input variable, i.e. the proportion of lost sugar beet roots that regrow in the following crop, as well as a series of parameters, mainly bolting rates and timing, timing and amount of flowering, pollen production and reproductive success.

2.2. Estimating groundkeeper parameters with field experiment

The objective of the present experiment was to estimate the life-cycle parameters for groundkeepers relative to weed beet, in different crops.

2.2.1. Experimental design

The experiment compared the growth and development of groundkeepers to that of weed beet in different crops in 2001–2002 and again in 2002–2003 at the INRA experimental station in Dijon-Epoisses (47.317°N, 5.017°E, 220 m altitude). The tested crops were winter wheat *(Triticum aestivum* L.), spring barley (*Hordeum vulgare* L.), spring pea (*Pisum sativum* L.), sugar beet and bare ground, the latter being the control without interspecific competition. Sugar beet was replaced by fodder radish (*Raphanus sativus* L.) in 2003. Each year, the five crops were randomized inside three blocks. Plots were 6 m × 12 m and 6 m × 13 m in 2002 and 2003, respectively. Tillage, pesticides and nitrogen were optimized for each crop. Details are given in Table 1..

2.2.2. Plant material

Weed beet seeds used in the experiments were the progeny of four weed beet populations (A, B, E and F) grown simultaneously in 2001 in a garden at Dijon, Burgundy, France (longitude 02°32′ E, latitude 45°18′ N, altitude 245 m). These populations descended from seed lots harvested in 1998 (Vigouroux, 2000) in North-Eastern France (longitude 04°03′ E, latitude 48°51′ N, altitude 83 m) (see details in Sester et al., 2004). The major difference between these populations was the weed beet density in the field where they were harvested.