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Mathematical Modelling of the biocontrol of *Rubus alceifolius*, an invasive plant in Réunion Island.

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Highlights: Invasive plants have become a major threat throughout the world, in particular in islands where the biodiversity is important and even unique. Since the 17th century, many weeds or invasive plants have been introduced in Réunion Island. Among them *Rubus alceifolius*, a giant bramble, is the most invasive and threatening to the endemic vegetation. After years of unsuccessful and even detrimental controls with herbicide applications and/or mechanical removal, a new biological control program has been launched, based on the release of a biocontrol agent, *Cibdela janthina*, a sawfly. Modelling Rubus-Cibdela interactions is not only helpfull to formalize knowledges but also to guide control strategies and decision-making, in particular before field releases. The aim of this talk, is to present a minimal mathematical model and some results based on ongoing experiments in Réunion Island.

Keywords: invasive plant, weed, biocontrol agent, plant-herbivore interaction, mathematical modelling, integro-differential equation, delay differential equation, qualitative analysis, simulation.

INTRODUCTION

Biological invasions, be they accidental or deliberate, currently constitute one of the main threat to biodiversity after habitat destruction and fragmentation. In particular invasive alien plants, like weeds, do not only impact biodiversity conservation, but can also reduce the quality and the quantity of agricultural products, with economic consequences. Thus, their control is an absolute necessity. Since the mid of the nineteenth century, classical biological control has proved to be a viable ecological solution to provide long-term control of invasive plants (Julien and Griffiths 1998). It is based on the importation and release of host-specific natural enemies (the biological agents). Weeds biological control is mainly used in Australia, New Zealand, Canada, South Africa and in the USA (Cruttwell McFadyen 1998), with relative good successes. Surprisingly, no biological control agents against alien plants have been released in Europe. One drawback of Control programs is that they need to be conducted over a period from ten to twenty years. Indeed, the effects of the control are not immediate and this may explain why biological control programs are declared failures or left. Mathematical modelling and, in particular, the qualitative study of the models, can be very helpful to hightligths all possible long-term dynamics according to weed-agent interactions, but also to the parameter values related to the weeds and the biocontrol agent. Moreover, it can also help to improve control strategies, using numerical simulations (Dumont et al. 2010, 2012).

Since human settlement in Réunion island (a volcanic island in the Indian Ocean) during the 17th century, various invasive plants have been introduced, but one is particularly invasive: the giant bramble, *Rubus alceifolius* Poir. (Rosaceae) (see Fig 1), which has been accidentalty introduced in the nineteenth century (and later in Queensland, Australia) and has spread throughout the island, from the Sea level to 1700 m. altitudes, due to its high plasticity and well adapted growth strategies (Baret 2002, Baret et al. 2004). Since the last thirty years, the main tools to control this weed have been pesticide applications and mechanical control or cutting control. However, Réunion island having a chaotic relief, it is not possible to treat all invaded areas. Moreover these control tools are not only inefficient but also costly. Thus, biological control is the only option that could reduce the impacts of this invasive alien plant. That is why a research program has been launched in 1997 to consider the so-called classical biocontrol: a biocontrol agent is released only once, assuming that it will establish and further releases will not be necessary. For *Rubus alceifolius* , after several studies, the selected biocontrol agent was *Cibdela janthina*. It is multivoltin sawfly, with 6 to 7 generations per year without diapause periods. The females lay eggs in batches, inside the main veins of young leaves at the apex of the plant. Only the larvae are phytopagous and can severaly defoliate R. alceifolius by consuming all leaves, except the thick middle veins and the petiole. Larvae have between five and seven feeding instars, depending on their sex and environmental parameters, but only the two last are big consumers of leaves (see Fig. 2).

After some preliminary studies between 2001 and 2007, *Cibdela janthina* has been selected and released in 2008 in the South-East part of la Réunion. Since then the Cibdela population has spread through the island. The first objective has also been reached: *Rubus alceifolius* has completely disappeared in some places (in particular at low altitudes), while in other places an equilibrium between Rubus and Cibdela has apparently been reached . Altogether, some unexpected situations appeared, and that is why new biological and ecological investigations have began two years ago. Field experiments are ongoing to provide parameters and study the impact of the altitude on the interaction between rubus and cibdela. In this context, and because we are first mainly interested in the long term behavior of the bramble biomass, when attacked by sawfly, at different altitudes, we start with a minimal (in the sense "less parameters as possible") Mathematical model. From our point of view, this is a first step towards more complex and detailed models, like Functional and Structural models, that require more precise knowledge on plant-pest interactions.

MINIMAL MATHEMATICAL MODELLING

Models related to the control of pest invasions by biocontrol agent are not numerous. For instance, in Chalak et al. (2011), the authors developed *discrete* deterministic and stochastic models to compare biocontrol made by two different agents: weevils and mycoherbicides. See also Stuart et al. (2002).

Here, since we are in mainly interested in the long term interactions between rubus and cibdela, we apply mathematical *continuous* modelling to model the biocontrol of *rubus alcefolius* or the Rubus-Cibdela interactions. We consider two main variables: B, the rubus biomass on a given surface, L the density of rubus density larvae. At this stage of our study, this two compartments model is « sufficient » in the case where we consider only rubus-cibdela interactions in a single domain, like a massif.

Our model is build as follows. Without biocontrol, rubus biomass is assumed to follow a logistic law, where r_0 is the net growth rate without cibdela, and B_{max} is related to the maximal biomass capacity of the massif. In the presence of cibdela, $r_1(L)$ becomes a nonlinear bounded and positive function, following the « Herbivory Optimization Hypothesis ». The damages caused by the larvae are modeled using a Holling functional response, $p(B)$. We assume that the time needed from feeding to newborns may vary from individual to individual, such that the larvae recruitment is $b\int_0^\infty e^{-m_L s}K(s)p\big(B(t-s)\big)L(t-s)\,ds$. b is the birth-rate, K(s) is a nonnegative probability distribution function representing the likelihood of taking time s to have offsprings, and $\int_0^\infty K(s)ds = 1$. m_L is the larvae death-rate, $e^{-m_L s}$ is the probability of an individual which starts to eat at time $t-s$ to be still alive at time t. Altogether, we derive the following system of integro-differential equations

$$\begin{cases} \frac{dB}{dt} = r_0 B(r_1(L)B_{max} - B) - p(B)L, \\ \frac{dL}{dt} = b\int_0^\infty e^{-m_L s}K(s)p\big(B(t-s)\big)L(t-s)\,ds - m_L L. \end{cases} \tag{1}$$

When $r_1(L) = 1$, and $K(s) = \delta_\tau(s)$, Model (1) reduces to a delay-differential equation that is well posed and has a unique positive solution (Gourley et al. 2005). Set $\mathcal{R} = \frac{fe^{-\eta m_L}p(B_{max})}{m} \leq 1$. If $\mathcal{R} \leq 1$, then system (1) will converge to $(B_{max}, 0)$. If $\mathcal{R} > 1$, then a positive equilibrium, (B^*, L^*), can exist. In the general case, depending on the values taken by τ and b, we show that system (1) can either develop a sustainable periodic behavior, or converge to (B^*, L^*), or even have a chaotic behavior, according to the parameter values.

Finally, based on recent results on cibdela biology (Mathieu et al., 2013), it may be possible to consider temperature (time) dependant parameters in model (1).

CONCLUSION

Despite their apparent simplicity, the previous models have complex dynamics that are able to reproduce various observed behaviors of rubus-cibdela interactions at different altitudes in Réunion Island: at low altitudes (below 350-400m), massif of rubus has almost disappeared, while above, rubus and cibdela populations seem to co-exist with various amplitudes, depending on the altitudes and the season. However numerous questions are still open: if other ressources for cibdela are available, how would the rubus-cibdela dynamic be affected. When attacked by cibdela, rubus consider several defenses mechanisms, like tolerance, using reserve biomass and/or increasing the production of seeds playing a great role in the renewal of rubus massif. Patch modelling may be also important to consider in order to connect rubus massifs at different altitudes. Another next stage in our study would be to refine plant-insect interactions, and then, using previous architectural studies (Fig. 1, Baret 2003), to derive a Plant-Insect FSPM model. If a rubus FSPM model seems to be feasible, taking into account knowledge on the bramble, additional studies are necessary to understand precisely the interactions between rubus and cibdela, in order to model them efficiently (see Lebon et al. 2013 for further investigations on plant defences and plant responses to (insect) herbivore attacks).

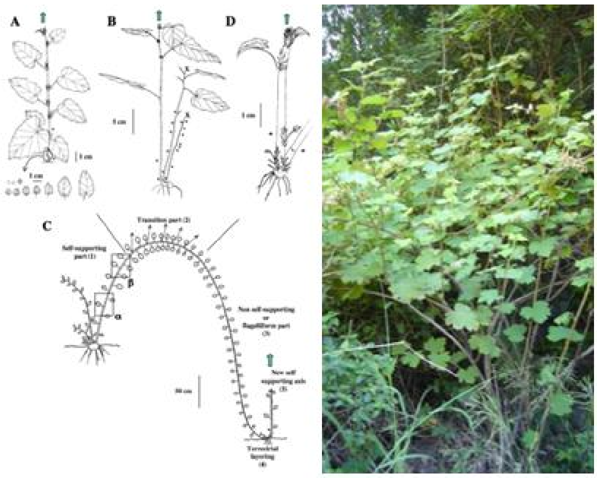

Fig. 1. *Rubus alceifolius* (Baret 2002; Baret et al. 2004)

Fig. 2. Larvae of *Cibdela janthina*… at work! (Mathieu et al., 2013)

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