Modeling the dynamics of woody plant–herbivore interactions with age-dependent toxicity

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Abstract In this paper we study the effects that woody plant chemical defenses may have on interactions between boreal hares that in winter feed almost entirely on twigs. We focus particularly on the fact that toxin concentration often varies with the age of twig segments. The model incorporates the fact that the woody internodes of the youngest segments of the twigs of the deciduous angiosperm species that these hares prefer to eat are more defended by toxins than the woody internodes of the older segments that subtend and support the younger segments. Thus, the per capita daily intake of the biomass of the older segments of twigs by hares is much higher than their intake of the biomass of the younger segments of twigs. This age-dependent toxicity of twig segments is modeled using age-structured model equations which are reduced to a system of delay differential equations involving multiple delays in the woody plant–hare dynamics. A novel aspect of the modeling was that it had to account for mortality of non-consumed younger twig segment biomass when older twig biomass was bitten off and consumed. Basic mathematical properties of the model are established together
with upper and lower bounds on the solutions. Necessary and sufficient conditions are found for the linear stability of the equilibrium in which the hare is extinct, and sufficient conditions are found for the global stability of this equilibrium. Numerical simulations confirmed the analytical results and demonstrated the existence of limit cycles over ranges of parameters reasonable for hares browsing on woody vegetation in boreal ecosystems. This showed that age dependence in plant chemical defenses has the capacity to cause hare–plant population cycles, a new result.

**Keywords** Plant–herbivore interactions · Woody plants · Plant chemical defense · Boreal ecosystem · Functional response · Age-structured model · Delay-differential equations · Time lag · Oscillations

**Mathematics Subject Classification (2010)** 34K13 · 34K20 · 34K25 · 34K60 · 92D40 · 92D50

1 Introduction

The early models of interactions between terrestrial plants and mammalian herbivores (e.g., Caughley 1976) tended not to differ from those models describing interactions between predators and animal prey or phytoplankton prey; that is, Rosenzweig–MacArthur type models, with Holling Type 2 functional responses. However, terrestrial plants differ from animal prey in a number of ways, including the obvious fact that typically only bite-sized parts of terrestrial plants are removed by herbivores. In recent years, specific plant characteristics have been taken into account in models. For example, it is known that the “quality” of plant material plays a major role in the interaction between the plants and herbivores. In particular, the nutrient:carbon ratios in plant biomass affect the feeding efficiency of the herbivore, which has been taken into account in Loladze et al. (2000) and subsequent papers.

Another plant characteristic is the variety of defenses that have evolved including chemicals that are toxic to herbivores known as plant secondary metabolites or PSMs (see reviews by Bryant and Kuropat 1980; Bryant et al. 1991b; Dearing et al. 2005; McLean and Duncan 2006; Torregrossa and Dearing 2009). Mammalian herbivores tend to regulate their intake of toxic PSMs to below deleterious (e.g., lethal) levels. This type of regulation is the foundation of pharmacological kinetics (pharmokinetics). An excellent review of the application of pharmokinetics to the feeding behavior of mammalian herbivores is by McLean and Duncan (2006). The production of PSMs and the feeding responses by mammalian herbivore has motivated the development of functional responses to take into account the combined effects of plant and mammal herbivore strategies. One of these is the so-called toxin-determined functional response model (acronym TDFRM; see Feng et al. 2008; Li et al. 2006; Liu et al. 2008; Feng et al. 2009). In particular, the TDFRM is a modification of the Holling Type 2 functional response; i.e.,

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f(N) = \frac{e\sigma N}{1 + h\sigma N}, \quad (1.1)
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