Pattern of storage and regrowth in ragwort

ED VAN DER MEIJDEN*, NICO J. DE BOER and CATHARINA A.M. VAN DER VEEN-VAN WIJK
Institute of Evolutionary and Ecological Sciences, Leiden University, Leiden, The Netherlands
(*author for correspondence, fax: +31-71-5274900, e-mail: meijden@rufsfb. leidenuniv.nl)

Received 14 June 2000; accepted 20 February 2001

Co-ordinating editor: T. Juenger

Abstract. Ragwort plants were damaged experimentally by removing the whole shoot. Within about 1 month the original allocation pattern of biomass to root and shoot was reestablished to a large extent. If left undisturbed for a longer period, plant growth accelerated into compensatory growth. Intraspecific variation in storage and tolerance (shoot weight), 1 month after damage, was significant. We could not detect a trade-off between storage or tolerance and relative growth rate of control plants. Consequently there are no indications for costs involved in storage of resources or in tolerating damage. Although tolerance is thought to be dependent upon storage of resources, we detected no effect of storage on tolerance after one event of damage. Storage is genotype specific, but at the same time highly plastic. We hypothesize that the value of storage in ragwort only becomes evident after repeated disturbances. Competition, history of herbivory and change of season all affected storage radically.

Key words: compensatory growth, competition, damage, herbivory, intraspecific variation, plasticity, storage of resources, tolerance

Introduction

All plant species suffer from a variety of abiotic disturbances like storm, frost and fire. Adaptations that reduce fitness loss due to this kind of damage, by storing resources in relatively safe organs to enable later regrowth, are widespread. There is an important difference between disturbances by abiotic and biotic agents, like pathogens and herbivores. In the case of an abiotic agent, continuation of damage is unrelated to what is left over of the plant; in the case of a biotic agent, continuation is likely to be related to (food quality and level and type of defence of) remaining tissue. The evolution of tolerance as a strategy to reduce the effect of herbivory should probably be seen as an extension of the general capacity to compensate for damage (Iwasa and Kubo, 1997). We define tolerance as the innate capacity of plants to reduce fitness loss due to loss of tissue (biomass, seeds, etc.) by damage. An operational definition of tolerance is the ratio of fitness (or another appropriate
parameter) between damaged plants and undamaged plants (Rausher, 1992; Simms and Triplett, 1994; Sadras and Fitt, 1997; De Jong and Van der Meijden, 2000). In this paper, we use the ratio between the weight of (parts) regrowing damaged plants and undamaged control plants of the same genotype to study tolerance experimentally by analyzing the process and pattern of regrowth.

Tolerance is thought to be dependent on stored resources (Van der Meijden et al., 1988; Iwasa and Kubo, 1997; De Jong and Van der Meijden, 2000). It is therefore a relevant question to ask: when does it make sense to store resources? Situations can be envisaged in which investment of resources in primary biomass does not result in growth. For deciduous trees, for instance, when the environment becomes too harsh for net growth, resources are stored. Under such circumstances storage has an advantage and is not costly in the sense that resources are withdrawn from plant growth. If storage is costly, a plant that will suffer from predictable damage by frost in winter should only store resources just before the period of yearly frost. A plant that, on the contrary, suffers from several unpredictable episodes per year of severe defoliation should always have some stored resources. If storage is costly, timing in relation to the predictability of the environment will be extremely important. We therefore expect plants to be plastic in their storage behavior. Here, we study benefits and costs of tolerance as well as intraspecific variation and plasticity of storage in relation to damage, competition, history of herbivory and seasonal change.

Two models have been developed to predict the optimal allocation of resources to storage for regrowth (Iwasa and Kubo, 1997; De Jong and Van der Meijden, 2000). These models assume that resources are withdrawn from the potential pool of resources of the production organ and thus predict a trade-off between relative growth rate (of undamaged control plants) and tolerance. A robust prediction from these models is that a plant should invest more in storage if the frequency or level of herbivory or other forms of damage is high.

Where to store resources? The answer is where the risk of loss is minimal. In general the root system of a plant is more sheltered against abiotic disturbances than other parts (Gulmon and Mooney, 1986). In five biennial plant species root herbivory was clearly less frequent than foliage herbivory (Van der Meijden et al., 1988). Tolerance of these species was positively related to their root/shoot ratio. In ragwort plants, aboveground regrowth following damage was positively correlated with root size (Van der Meijden and Van der Waals-Kooi, 1979). In several other studies it was found that regrowth capacity after damage was related to the amount of stored carbohydrates or other substances like nitrogen (Chapin III et al., 1990; Volence et al., 1996). We define allocation to storage as root weight divided by total plant weight.