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Review

Biological control and nutrition: Food for thought

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HIGHLIGHTS

- This is a review paper on the effect of nutrition on producing biocontrol agents.
- We focused on biological control agents used to control insect pests.
- We examined nutritional impacts on biocontrol traits in a variety of biocontrol agents.
- Based on the literature nutrition plays a major role in the success of a biocontrol agent.

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ABSTRACT

Biological control agents including a wide range of organisms such as predators, parasitoids, and entomopathogens (bacteria, fungi, nematodes, and viruses) are frequently used to control insect pests. Despite commercial availability of these biocontrol agents their widespread use is limited due to biological and economic difficulties. Efficient mass-production relies heavily on the environment in which the agent is grown. Nutrition can play a significant role in important biocontrol traits such as colonization and survival, tolerance to environmental stress, reproduction, and longevity. Therefore, to increase biocontrol potential nutritional aspects should be considered prior to commercial production. This review aims to explore the role nutrition plays in the production and efficacy of biocontrol agents by summarizing the effect nutrition has on important biocontrol traits, specifically traits in organisms that target insect pests including predators, parasitoids, and microbial agents.

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1. Introduction

Chemical pesticides have been commonly used since the mid-twentieth century and their application has increased ever since. An estimated 500 million kg are applied annually in the U.S. and about 3 billion kg are applied worldwide (Pimentel, 2005). High application rates have introduced new problems including secondary pest outbreaks, resistance, and hazards to the environment and human health (Pimentel, 2005). Due to these risks and strict regulations on chemical pesticides, more thoughtful pest control efforts are increasingly incorporating biological control (Chandler et al., 2011; Czaja et al., 2015; Glare et al., 2012; Kogan, 1998).

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Typically, there are four types of biological control: classical, inundative, inoculative, and conservation. In classical biological control the focus is on invasive pests. A natural enemy is collected at the location from which the pest originates and introduced into the new environment to control the invasive pest species; the expectation is that the introduced organism will become permanently established. Inundative biological control consists of mass-production of the natural enemy and widespread distribution in the environment to suppress the pest without permanent colonization of the released biocontrol agent (the approach is similar to how most standard chemical insecticides are employed). Inoculative biological control can be considered intermediate between classical and inundative approaches; the natural enemy is released with the expectation of some recycling though not permanent establishment, and thus the organism is released again after several seasons or years. Finally, conservation biological control is the practice of protecting natural enemies in the environment.

Diverse organisms have been investigated for use in biological control including insect parasitoids and predators and entomopathogens, which include bacteria, viruses, fungi, and nematodes. Many of these organisms are commercially produced and have widespread use for inoculative and inundative biological control. However, due to varying host-ranges, variable field efficacy, and practicality many biological control agents have had limited success and require further optimization. Despite the time and resources spent investigating biological control agents, only some have been used extensively (Chandler et al., 2011; Pedigo and Rice, 2009; Shapiro-Ilan et al., 2002; Vega and Kaya, 2012).

The infrequent use of biological control agents in general is due to economic as well as biological obstacles. Lidert (2001) suggested that the lack of biological pesticide products stems from insufficient understanding of market needs and strategy, cost efficiency, and shelf-life stability. Additionally, the range (broad or narrow) of hosts affected by biological agents and the ability to be mass-produced influence the success of these products. Ultimately, for biological control methods to be more widely adopted their benefits must outweigh their costs.

Increasing the successful use of biological agents in classical, inundative or inoculative approaches requires efficient mass-production methods. However, isolating an organism and rearing it in the laboratory can lead to the deterioration of traits required for success in the field. For example, numerous hymenopteran parasitoids used in biological control have been reported to decrease in host acceptance, fecundity, and longevity after long periods (generations) in the laboratory (Geden et al., 1992; Rojas et al., 1999; van Bergeijk et al., 1989). It has been shown that laboratory-reared entomopathogenic nematodes (EPNs) can lose their ability to find, infect, and kill their insect host, have decreased fecundity, and are less tolerant to environmental stress (Bilgrami et al., 2006). Sub-culturing has resulted in the reduced virulence of biological control agents such as viruses, bacteria, and entomopathogenic fungi (Dulmage and Rhodes, 1971; MacKinnon et al., 1974; Tanada and Kaya, 1993; Vandenberg and Cantone, 2004). Observed deterioration has been attributed to genetic factors such as drift, inbreeding, and inadvertent selection (Bai et al., 2005; Chaston et al., 2011; Hopper et al., 1993; Hoy, 1985; Roush, 1990). However, these problems may also be driven, either alone, or in combination with non-genetic factors such as disease and nutrition (Hopper et al., 1993).

While not much effort has gone into determining the effect nutrition has on trait deterioration, several studies have investigated the role of nutrition on the efficacy of various biological control agents. This review aims to highlight the role nutrition plays in the production and efficacy of entomopathogenic biocontrol agents (predators, parasasitoids, bacteria, fungi, viruses, and nematodes); specifically, the effect of nutrition on important biocontrol traits such as environmental tolerance and survival, reproductive potential, longevity, and virulence. Our intent is to provide examples that demonstrate the importance of understanding nutritional aspects of producing biocontrol agents.

1.1. Mass production

An in-depth look at mass-production of biocontrol agents is beyond the intended scope of this review; however, understanding the methods used to culture these organisms is important for determining how these methods affect their efficacy. Production, formulation, and delivery have been reviewed extensively elsewhere (Ehlers, 2001; Fravel, 2005; Morales-Ramos et al., 2014; Vega and Kaya, 2012). Production of biocontrol agents can be achieved using *in vitro* or *in vivo* methods. For example, EPNs can be reared *in vivo* by inoculating insect hosts and harvesting the nematodes from host cadavers, or reared on their symbiotic bacteria using *in vitro* solid or liquid cultures (Shapiro-Ilan et al., 2012b). Agents that are amenable to liquid culture such as EPNs, bacteria, and fungi typically begin in medium-sized flasks and are scaled-up to large fermentors (4000 L or more) (Ehlers, 2001; Fravel, 2005).

Large-scale production of predators and parasitoids can be significantly more complicated. Most are reared on artificial diets, which often requires supplementation with honey or sugar solutions (Thompson, 1999). Additionally, many parasitoids feed on host hemolymph and plant material. If artificial diets are unavailable or not possible, these insects must be reared on their natural host in addition to the host's natural plant food. Due to cost considerations, a factitious host is often used rather than the natural host; however, this tradeoff can have negative effects on fecundity, lifespan, and other traits (Bai et al., 1992; Bigler et al., 1987; Kazmer and Luck, 1995).

The major limiting factors in mass production of biological control agents are the costs associated with growth substrates, low reproductive rates, and/or limited economies of scale (Fravel, 2005). *In vivo* methods are often significantly more expensive than *in vitro* methods and are difficult to scale up. However, for most organisms, technological improvements continue to make *in vivo* production more feasible (Gaugler et al., 2002). In each case methods must be carefully assessed and optimized individually before commercialization of a biocontrol agent is plausible.

2. Nutritional effects on biocontrol traits

Although the field of molecular genetics has revolutionized our understanding of the relationship between genotype and phenotype, the role that the environment plays in gene expression and, ultimately, the phenotype of an organism, is frequently underappreciated. When an organism is isolated from its natural environment and reared in the laboratory, it is important to understand how laboratory conditions and/or nutrition can affect the organism's ability to control insect pests. The following sections will discuss how nutrition affects important traits in biocontrol agents used to control insect pests. There are many traits that make an organism suitable for mass production and subsequent field and glasshouse applications to combat agricultural pests and diseases. These traits include, but are not limited to, survival and tolerance to environmental stress, reproductive potential, and infectivity or virulence.

2.1. Predators and parasitoids

Over the past half-century insect parasitoid and predator studies have emphasized growth on artificial diets. Rearing these