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The role of interference competition in a sustained population outbreak of the aspen leaf miner in Alaska

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Abstract

Direct density-dependence through intraspecific competition may be an important mechanism permitting sustained herbivore outbreaks. In theory, interference competition could allow a relatively stable number of herbivore individuals to survive while moderating host plant damage. This research examined the potential role of intraspecific competition in permitting a decade-long outbreak of the aspen leaf miner, *Phyllocnistis populiella*, on *Populus tremuloides* in interior Alaska. A combination of observational and experimental studies examined larval food requirements, food resources, and the impacts of *P. populiella* larval density on survival, mass, and leaf mining damage. These results were then compared to those from nine years of survey data examining the density of eggs and pupal chambers, as well as leaf mining damage. The number of *P. populiella* eggs per leaf surface often exceeded the number that could be supported through larval development. Consistent with the expectations of interference competition, the probability of larval survival displayed a decelerating decline with increasing density. Pupal mass of surviving individuals was not related to larval density suggesting little impact of exploitative competition. Mean percent of leaf area mined saturated between 65 and 75%. Taken together these results suggest that strong interference competition largely precludes exploitative competition in *P. populiella* larvae thereby allowing some individuals to survive and attain normal pupal size even when densities far surpass the carrying capacity of the resource. Interference competition also limits host plant damage thereby contributing to the preservation of a healthy resource base. By constraining both larval survival and host plant damage, interference competition may foster the maintenance of sustained outbreaks of *P. populiella*.

Zusammenfassung

Direkte Dichteabhängigkeit durch intraspezifische Konkurrenz kann ein wichtiger Mechanismus sein, der dauerhafte Massenentwicklung von Herbivoren ermöglicht. Theoretisch könnte Interferenz einer relativ stabilen Zahl von Herbivoren erlauben zu überleben, während der Schaden an der Wirtspflanze gemildert wird. Diese Studie untersuchte die potentielle Rolle der intraspezifischen Konkurrenz für die Ermöglichung einer 10-jährigen Massenentwicklung des Gemeinen Pappelblattminierers, *Phyllocnistis populiella*, auf *Populus tremuloides* in Zentralalaska. In einer Kombination von Beobachtungen und Experimenten untersuchten wir die Nahrungsansprüche der Larven, die Nahrungsressourcen und den Einfluss der Larvenabundanz des Minierers auf die Überlebensrate, Masse und Blattschaden. Diese Ergebnisse wurden dann verglichen mit denen einer neunjährigen Erfassung der Abundanzen von Eiern und Puppenkammern sowie des Blattschadens. Die Zahl der *P. populiella*-Eier pro Blatt überstieg oft die Zahl der Larven, die ihre Entwicklung dort vollenden konnten. In Übereinstimmung mit den Erwartungen für die Interferenz, zeigte die Überlebenswahrscheinlichkeit der Larven einen Abfall mit steigender Larvendichte. Die

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Puppenmasse der überlebenden Individuen zeigte keinen Bezug zur Larvendichte, was auf einen geringen Einfluss der exploitativen Konkurrenz hindeutet. Bis zu 65 bis 75% der Blattfläche wurden miniert. Zusammengenommen legen diese Ergebnisse nahe, dass Interferenz weitgehend exploitative Konkurenz unter *P. populiella*-Larven ausschließt, wodurch einige Individuen überleben und die normale Puppengröße erreichen können, sogar wenn die Individuendichten die Kapazität der Nahrungsressource bei weitem überschreiten. Interferenz begrenzt auch den Schaden für die Wirtspflanze, was zum Erhalt einer funktionstüchtigen Ressourcenbasis beiträgt. Indem sowohl die Überlebensrate der Larven als auch der Schaden an der Wirtspflanze begrenzt wird, kann Interferenz die Aufrechterhaltung von dauerhaften Massenentwicklungen von *P. populiella* unterstützen.

Keywords: Boreal forest; Contest competition; Herbivory; Plant–insect interactions; Population regulation

Introduction

Intraspecific competition can have important feedbacks on population dynamics and interspecific interactions (Haukioja, Kapiainen, Niemelä, & Tuomi 1983; Berryman 1987; Myers 1988; Abbott & Dwyer 2007). Berryman (1987) proposes that sustained herbivore outbreaks result when direct negative density dependence occurs at high population density thereby allowing the maintenance of insect and host populations. Interference competition has the potential to cap the number of surviving individuals and provide this density dependent feedback. If interference reduces herbivore densities prior to strong exploitative competition, it may limit host plant damage and allow surviving herbivores to acquire adequate resources to maintain quality. These feedbacks may allow the maintenance of healthy herbivore and host plant populations across multiple years of high herbivore density.

We were interested in whether intraspecific interference competition was moderating feedbacks in an herbivore that experiences sustained outbreaks. *Phyllocnistis populiella* Chambers (Lepidoptera: Gracillariidae), the aspen leaf miner, is a widespread herbivore of quaking aspen, *Populus tremuloides* Michx. The leaf miner normally occurs at low population densities (<1 mine/tree; personal observation). However, spatially stable *P. populiella* outbreaks can persist for a decade or more over large regions (Condrashoff 1964; USDA Forest Service 2012; Yukon Energy, Mines and Resources, Forest Management Branch 2012). The palearctic congener, *Phyllocnistis labyrinthella*, also persists at high population densities on European aspen, *Populus tremula*, for extended periods of time (Sundby 1953; Albrectsen et al. 2010). *P. populiella* caused extensive damage to interior Alaska aspen stands from 2002 to 2012 (USDA Forest Service 2012). During the outbreak *P. populiella* displayed little if any discrimination among host plant individuals resulting in heavy damage to all trees. On average, aspen saplings surveyed in 2004–2011 had 45% of their leaf area mined. Mature aspen trees suffered even greater mining damage; in 2006 saplings and mature trees experienced 49 and 70% leaf area mined, respectively.

Leaf mining species often experience strong intraspecific larval competition because larval movement restricted to the immediate vicinity of the oviposition site limits the reduction of competition through dispersal (Connor & Taverner 1997). While most leaf miner populations seldom if ever reach densities where intraspecific competition becomes important, a quarter of the species considered by Auerbach, Connor and Mopper (1995) either experienced population outbreaks or persisted at high densities. In outbreaking populations of leaf miners, only intraspecific competition impacting larval survival and/or pupal mass commonly acts in a negative density-dependent manner and thus has the potential to regulate populations (Auerbach et al. 1995).

P. populiella provides a good system for examining the impacts of intraspecific competition on herbivores and their host plants. Larvae are restricted to feeding on a single leaf surface, and during outbreaks, the number of *P. populiella* eggs laid per leaf surface may exceed the number of larvae that can be supported through development. Interference competition occurring early in development has the potential to reduce overall plant damage and thereby ensure adequate food for the growth of surviving individuals.

We hypothesized that intraspecific interference competition had the potential to regulate *P. populiella* populations and moderate host plant damage thereby fostering sustained outbreaks. We used a combination of field experiments, observational studies, and broader surveys during an outbreak of *P. populiella* to address the following questions:

(1) Do *P. populiella* larvae experience intraspecific competition as indicated by initial densities that exceed food availability and a negative effect of density on larval performance?
(2) Do *P. populiella* larvae experience interference competition as indicated by a decelerating decline in survival probability with increasing density?
(3) Do *P. populiella* larvae experience exploitative competition as indicated by a negative relationship between density and the mass of surviving *P. populiella* individuals?
(4) Does leaf mining damage asymptote below 100% with increasing *P. populiella* density?