Forest Ecology and Management 415–416 (2018) 118–128

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Small herbivore exclosure cages alter microclimate conditions

Piers Evans[a,*], Emma L. Davis[b], Ze'ev Gedalof[b], Carissa D. Brown[a]

[a] Department of Geography, Memorial University, 230 Elizabeth Avenue, St. John's, Newfoundland and Labrador A1B 3X9, Canada
[b] Department of Geography, University of Guelph, 50 Stone Road East, Guelph, Ontario N1G 2W1, Canada

ARTICLE INFO

Keywords:
Cage
Forest
Herbivore exclosure
Microclimate
Seed predation
Vertebrates

1. Introduction

Climate and edaphic characteristics are the dominant drivers of species distributions, yet it is becoming increasingly apparent that plant and animal distributions are also shaped by local intra- and inter-specific biotic interactions (HilleRisLambers et al., 2013) such as competition (Tingstad et al., 2015), predation (Brown and Vellend, 2014; Johnson and Fryer, 1996), facilitation (Bruno et al., 2003), and mutualisms (Nuñez et al., 2009). Sessile terrestrial plants are unable to effectively evade herbivores, and are therefore vulnerable to herbivory and seed predation by vertebrates and invertebrates. Predicting the magnitude of the effects of biotic interactions on a species' ability to respond to climate change is challenging given that biotic interactions are inherently tied to local abiotic environmental gradients. Experimental field studies are necessary to tease apart biotic and abiotic (i.e., climatic, edaphic) processes controlling the distributions of species (HilleRisLambers et al., 2013). The methodologies employed in this ongoing investigation have, however, received little scrutiny thus far.

The use of herbivore exclosure devices in field experiments has become a popular means of assessing the effects of herbivory, by both post-dispersal seed predators and plant herbivores, on recruitment and plant community dynamics. Such effects are of strong interest in conservation biology, where plant-herbivore interactions between native and introduced species are often important (Boyd et al., 2017; Forsyth et al., 2015; Hager and Stewart, 2013; Thompson et al., 1992), and for forestry and horticultural applications, where herbivory and seed predation can constrain productivity (Leadem et al., 1997; Marsh et al., 1990). The benefits of using exclosures in field-based herbivore-plant interaction research are obvious: exerting control over a natural system by experimentally manipulating conditions in the field can isolate the impacts of a group of herbivores on a selected area and/or plant species, whereas observational studies must rely more heavily on inference. However, exclosure studies have been criticised for not addressing fundamental interactions between herbivore groups and the species they consume, and instead apply a binary filter on a complex relationship (Hester et al., 2000). Nevertheless, exclosure studies produce consistent responses among prey species the vast majority of the time (Sih et al., 1985). The prevalence of significant effect size, as well as the immutable importance of herbivore-plant interactions research (Humphrey, 1998), explains the continued popularity of herbivore exclosure studies, despite often being logistically challenging.

Alternatives to using herbivore exclosures in experimental herbivore-plant interaction studies are uncommon in the literature. Lab-based research focussed on herbivore-plant interactions can be practical when looking at herbivore-induced reactions in plants (e.g., Roslin et al., 2008; Hartley and DeGabriel, 2016), or when a plant and its respective herbivore specialist can be tested in a lab (e.g., Bates et al., 2000); however, these options are not always feasible and such research often requires field-based experimental data collection. Camera traps, a method borrowed from wildlife studies (Kucera and Barrett, 2011; Trolliet et al., 2014), have been effectively used in herbivore-plant interaction studies to identify herbivores (Nuñez et al., 2008) and observe their behaviour (Jansen et al., 2012). Their use in plant-focussed research remains limited (Burton et al., 2015), however, due to their inability to quantify aspects of herbivore-plant interactions such as the extent of damage caused by browse pressure (Brodie et al., 2012; Kuijper et al., 2009).

Abbreviations: SBC, small box cage; LBC, large box cage; LRC, large round cage

* Corresponding author.
E-mail addresses: pe7572@mun.ca (P. Evans), edavis02@uoguelph.ca (E.L. Davis), zgedalof@uoguelph.ca (Z. Gedalof), carissa.brown@mun.ca (C.D. Brown).

https://doi.org/10.1016/j.foreco.2018.02.012
Received 12 December 2017; Received in revised form 5 February 2018; Accepted 8 February 2018
0378-1127/

Table 1
A sample of the variety of designs and range of sizes of herbivore exclosures used in herbivory studies. "Open or closed" refers to the exclosure's top; Ø refers to a diameter measurement. Citations: (1) Mittelbach and Gross (1984), (2) Brown and Vellend (2014), (3) Cassin and Kotanen (2016), (4) Côté et al. (2005), (5) Smart et al. (1998), (6) Meng et al. (2012), (7) DeMattia et al. (2004), (8) Forsyth et al. (2015), (9) Pastor et al. (1993), and (10) Thompson et al. (1992).

Type	Target species group	Dimensions of exclosure	Open or closed	Materials used	Habitat; location	Duration	Reference
Cage	Small rodents	20 × 20 × 5 cm	Assumed closed	6 mm wire mesh	Old-field habitat; Southwestern Michigan, USA	July 1983	(1)
Cage	Small rodents	20 × 20 × 20 cm	Closed	1 cm hardware cloth, stainless steel nails	Mixedwood Appalachian forest; Southern Quebec, Canada	Oct 2012 – April 2013	(2)
Cage	Small rodents	25 cm × 36 cm Ø	Closed	1.25 cm^2 hardware cloth, PVC pipe, metal flashing	Scientific reserve within mixedwood plains ecozone; South-central Ontario, Canada	August – October 2013	(3)
Cage	Small vertebrates	90 × 90 × 60 cm	Closed	6.4 mm galvanised wire mesh	Boreal forest; South-central Quebec, Canada	June – August 2001	(4)
Cage	Aquatic reptiles and fish	90 cm Ø × 122 cm	Closed	5 × 10 cm welded wire fencing, rebar, wire ties	Lake and shoreline habitat; Southern Texas, USA	June – Sept 1996	(5)
Net	Avi-fauna	Varied	Closed	20 mm black nylon netting, bamboo stakes	Tropical rainforest; Southern Yunnan Province, China	April – May 2004	(6)
Cage	Rodents and large mammals	4 m Ø × 1.5 m	Closed	Wire fencing (dimensions unspecified)	Tropical wet forest; Costa Rica	Feb 2001 – July 2002	(7)
Fence	Deer	12 × 12 × 2 m	Open	2 m posts and 10 × 10 cm mesh	Mixed conifer-angiosperm forest; Southern South Island, New Zealand	July 2004 – July 2006	(8)
Fence	Moose	15 × 15 × 3 m	Open	Wire fencing (dimensions unspecified), cedar posts	Boreal forest; Isle Royale, Michigan, USA	Approx. 1950 – 1988	(9)
Fence	Moose	15 × 15 m	Open	Materials and dimensions unspecified	Boreal forest; East-central Newfoundland, Canada	1976 – 1987	(10)

The design of herbivore exclosures must be scaled to the consumers of interest in a given study, such that a wide range of sizes, designs, and materials are commonly employed (Table 1). Though there exists an extensive body of literature regarding the effects of large herbivores on various plant species (e.g., McLaren et al., 2009; Kain et al., 2011; Ellis and Leroux, 2017), our focus in this study is on herbivore exclosure cages intended to exclude small vertebrate animals (e.g., Mittelbach and Gross, 1984; Côté et al., 2005; Brown and Vellend, 2014). The majority of literature describing the use of exclosures (Bowers, 1993; Fraser and Madson, 2008; Olofsson et al., 2004; Young et al., 1997) provides adequate information for the replication of their designs and deployment techniques and this is supplemented by forestry (Leadem et al., 1997) and field operations manuals (O'Keefe and Alard, 2002). Yet, the body of literature evaluating design considerations of herbivore exclosures appears sparse.

Although the materials used in vertebrate exclosure cages appear largely consistent (Table 1), the impact of material and design selection on the conditions within and in immediate proximity to the exclosure has, to our knowledge, not been investigated under snowy winter conditions. Tree guard effects on microclimate conditions have been investigated during the growing season (e.g., *Prunus* plantation, south of France, Bergez and Dupraz, 2000; *Eucalyptus-Banksia-Allocasuarina* woodland, southwestern Australia, Close et al., 2009; experimental *Quercus* plantation, southwestern Washington, Devine and Harrington, 2008), however the influence of this type of exclosure on snow and over-winter conditions appears yet to be studied. Researchers that manipulate highly localised temperature regimes to observe plant responses (e.g., International Tundra Experiment) have developed methods to maximise control over temperature ranges within an enclosure (Chapin and Shaver, 1985; Henry and Molau, 1997; Marion, 1996). However, we assert that in small herbivore exclosure experiments, the alteration of microclimate conditions is an inadvertent outcome of the methodologically standard practise of placing a barrier between small herbivores and their potential prey. This is problematic because differences in plant performance between control and exclosure plots are typically attributed solely to the effects of herbivory, when unanticipated and unaccounted for differences in microclimate may confound these results.

Microclimate modification within small herbivore exclosure cages (hereafter, 'exclosures' or 'cages') could occur in various settings, however we posit that unintended effects are likely most pronounced when cages are deployed in areas that experience seasonal snow accumulation. Slight temperature differences within exclosures could affect initial snow accumulation and the later release from snow cover, with consequences for the performance of vegetation. For example, small changes in the duration of snow cover can significantly affect the germination, growth, and survival of juvenile plants, which can benefit from the protection provided by snow cover (Renard et al., 2016). Alternatively, exclosure walls may reduce surface wind speeds, or act as snow fences, leading to increased snow accumulation in their immediate vicinity (Wipf and Rixen, 2010). In an effort to quantify the effects of cages on microclimate conditions, we deployed field experiments in three geographically distinct environments to test whether (1) the onset of winter, marked by the first accumulation of snow lasting 24 h, occurred later and was marked by colder temperatures within cages than without, (2) spring thaw, marked by the last accumulation of snow lasting 24 h, occurred earlier and was marked by colder temperatures within cages than without, and (3) the number of snow-covered days during the winter was fewer within cages than surrounding areas. Further, we investigated how construction material and design influenced the degree of microclimate modification. Alteration of microclimate conditions within cages has important implications for