

OIKOS

Meta analysis

Global patterns of insect herbivory in gap and understorey environments, and their implications for woody plant carbon storage

Frida I. Piper, Scott H. Altmann and Christopher H. Lusk

F. I. Piper (<http://orcid.org/0000-0002-8220-073X>)(fpiper@ciep.cl), Centro de Investigación en Ecosistemas de la Patagonia (CIEP), Moraleda 16, Coyhaique, Chile. – S. H. Altmann, Independent Research Ecologist, Binghamton, NY, USA. – C. H. Lusk, Environmental Research Inst., The Univ. of Waikato, Hamilton, New Zealand.

Oikos

00: 1–14, 2018

doi: 10.1111/oik.04686

Subject Editor: Lonnie Aarssen

Editor-in-Chief: Dries Bonte

Accepted 1 December 2017

Insect herbivory is thought to favour carbon allocation to storage in juveniles of shade-tolerant trees. This argument assumes that insect herbivory in the understorey is sufficiently intense as to select for storage; however, understoreys might be less attractive to insect herbivores than canopy gaps, because of low resource availability and – at temperate latitudes – low temperatures. Although empirical studies show that shade-tolerant species in tropical forests do allocate more photosynthate to storage than their light-demanding associates, the same pattern has not been consistently observed in temperate forests. Does this reflect a latitudinal trend in the relative activity of insect herbivory in gap versus understorey environments? To date there has been no global review of the effect of light environment on insect herbivory in forests. We postulated that if temperature is the primary factor limiting insect herbivory, the effect of gaps on rates of insect herbivory should be more evident in temperate than in tropical forests; due to low growing season temperatures in the oceanic temperate forests of the Southern Hemisphere, the effect of gaps on insect herbivory rates should in turn be stronger there than in the more continental temperate climates of the Northern Hemisphere. We examined global patterns of insect herbivory in gaps versus understoreys through meta-analysis of 87 conspecific comparisons of leaf damage in contrasting light environments. Overall, insect herbivory in gaps was significantly higher than in the understorey; insect herbivory was 50% higher in gaps than in understoreys of tropical forests but did not differ significantly between gaps and understoreys in temperate forests of either hemisphere. Results are consistent with the idea that low resource availability – and not temperature – limits insect herbivore activity in forest understoreys, especially in the tropics, and suggest the selective influence of insect herbivory on late-successional tree species may have been over-estimated.

Keywords: shade tolerance, herbivory tolerance, meta-analysis, forest dynamics, latitudinal gradient



© 2017 The Authors. Oikos © 2017 Nordic Society Oikos

Introduction

Insect herbivory is thought to exert important selective pressures on the traits of late-successional tree species. A carbon conservation strategy of allocation to storage and defences at the expense of growth is considered critical for low-light survival (Coley et al. 1985, Myers and Kitajima 2007, Poorter et al. 2010): to persist in the understorey, plants must be able to recover from herbivory through mobilization of stored carbohydrates (Kitajima 1994, Kobe 1997, Walters and Reich 1999). This strategy is also known as herbivory tolerance, and it is assumed to relate to heavy herbivory pressure and severe damage (Rosenthal and Kotanen 1994, Rosenthal and Welter 1995, Tiffin and Rausher 1999). Thus, the view that conservative carbon allocation is fundamental for low-light success assumes that understorey insect herbivory is high enough as to select for herbivory tolerance.

Although some studies have found evidence linking seedling shade tolerance to carbon allocation to storage (Canham et al. 1999, Kitajima 1994, Poorter and Kitajima 2007), several others did not (Canham et al. 1999, Lusk and Piper 2007, Piper 2015, Piper et al. 2009, 2017). One possible explanation for the discrepancy is that, in some regions, the levels of understorey herbivory are insufficient to select for herbivory tolerance. Although many studies have examined the influence of light environment on insect herbivory (Niesenbaum 1992, Niesenbaum et al. 2006, Guerra et al. 2010, Salgado-Luarte and Gianoli 2010), at present we lack an overview of levels of insect herbivory damage in contrasting light environments at regional and global scales. Such an assessment would improve our understanding of selective pressures on plant traits in relation to light environment.

Light environment may affect insect herbivory through its influence on insect body temperatures (Andrew et al. 2012). As insects are ectotherms, their metabolism and feeding rates are sensitive to small variations in environmental temperature (Frazier et al. 2006). In general, low temperatures reduce the growth, survival and consumption rates of insect herbivores (Scriber and Slansky 1981, Lindroth et al. 1997, Levesque et al. 2002, Paritsis and Veblen 2010). Since well-lit leaves are often several degrees warmer than those in the understorey (Percy 1987, Naidu and DeLucia 1998), low-light environments could involve temperature limitations for herbivores in temperate regions; ectotherms do in fact move among different light environments for thermoregulation (Heinrich 1995, Schultz 1998). Given that air temperature decreases in general with latitude, but that the optimal temperature range for insect metabolism is similar across latitudes (Tauber et al. 1987, Frazier et al. 2006, Deutsch et al. 2008, Huey 2010), the search for sunny, warm spots will be more important in temperate than in tropical regions. Notably, while many studies have used latitude to test for temperature effects on global pattern of herbivory (del-Val and Armesto 2010, Garibaldi et al. 2011, Moles et al. 2011, Zhang et al. 2011), no one appears to have considered the influence of light as a moderator of temperature (Fig. 1). An interactive

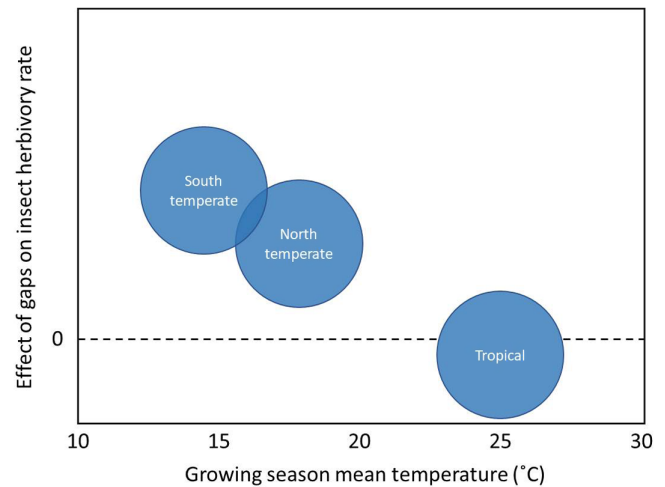


Figure 1. Graphical representation of our first hypothesis, showing predicted effects of growing season mean temperature on the effect of light environment on insect herbivory across different climate types, assuming similar optimum temperatures for insect herbivores across biomes (Frazier et al. 2006, Huey 2010). y-axis shows predicted effect of canopy gaps on herbivory rates in different climate types: insect herbivores are most likely to prefer well-lit environments (gaps) in the oceanic temperate climates of the Southern Hemisphere, where low growing-season temperatures (Lieth et al. 1999) may result in understorey temperatures being well below the optimum for insect metabolism.

effect of light and latitude on herbivory would have important implications for the physiological ecology of forest succession. For example, insect herbivory in the understorey of temperate forests might be insufficient to favour the evolution of herbivory tolerance in shade-tolerant late-successional species – especially in the Southern Hemisphere, where oceanic climates result in lower average growing-season temperatures than in the continental climates of the Northern Hemisphere (Lieth et al. 1999). In contrast, as temperatures in tropical climates are close to the optimum for insect performance (Deutsch et al. 2008), insect herbivory levels may be high enough to select for herbivory tolerance (Kitajima 1994, Myers and Kitajima 2007). In the tropics, herbivores might even prefer the understorey because gaps might expose them to excessive radiative heating (Fig. 1).

Light environment might affect herbivory through its influence on resource availability. Primary productivity in gaps is higher than in understoreys because plant growth is strongly light-limited in understoreys (Augsburger 1984, King 1994, Richards and Coley 2007). In some cases, higher light availability also increases leaf nutrient concentrations (e.g. nitrogen) (Osier and Jennings 2007) (but see Lusk and Reich 2000). Well-lit environments may thus attract more insect herbivores than understoreys because of much more abundant and possibly more nutritious foliage (Richards and Coley 2008); this might lead to higher herbivory rates (Richards and Coley 2007). Gaps have especially pronounced effects on the biomass of light-demanding, fast-growing

plants, which respond more strongly to light than shade-tolerant, slow-growing species (Kitajima 1994). On the other hand, chemical and physical defences have been found to increase with light availability (Niesenbaum 1992, Chacón and Armesto 2006, Niesenbaum and Kluger 2006, Salgado-Luarte and Gianoli 2010, Sinimbu et al. 2012), which could lead to the opposite pattern: higher herbivory rates in low-light environments.

In this paper we assess global patterns in the influence of light availability on the incidence of insect damage to leaves, and discuss the implications for plant carbon storage. We gathered studies quantifying insect herbivory within plant species (i.e. intra-specific level) in contrasting light environments, and then conducted a meta-analysis to explore patterns within and across major climatic regions. We considered three hypotheses about controls on global and regional patterns in herbivory. First, that temperature limitation is the primary control on patterns of insect herbivory; in this case the relative importance of understorey herbivory should decrease with latitude, with insect herbivory being higher in gaps than in understoreys in temperate forests – especially in the oceanic climates of the Southern Hemisphere (Fig. 1). We saw less reason to expect such differences between gap and understorey environments in tropical forests, although we considered that insect herbivores might be stressed by radiative heating in high-light environments (Deutsch et al. 2008) (Fig. 1). Second, we examined the hypothesis that herbivore activity is primarily a function of resource availability (Richards and Coley 2007); in this case, herbivory rates should be higher in gaps than in understoreys regardless of latitude and climate, because of the greater productivity of well-lit environments. If present, such a pattern should be more pronounced in light-demanding species than in shade-tolerant associates. Finally, leaf palatability could be the primary control on patterns of insect herbivory; in this case herbivory rates should be lower in gaps than in understoreys, regardless of climate and latitude.

Methodological approach

Literature searches

We conducted a first search on the Web of Science (accessed 25 April 2014) and a second one at 24 April 2016 looking for any type of study in English or Spanish that analysed insect herbivory of plants in sun and shade environments. Specifically, we searched abstracts using the following combination of words: 'herbivory* AND light* AND forest*'. We found 425 studies from which we discarded those using artificial shade, simulated herbivory, non-insect herbivory (e.g. deer browsing), and aquatic herbivory. To be included in our meta-analysis a study should 1) quantify insect herbivory of a terrestrial plant (a single species or group of species) growing naturally under at least two contrasting light environments within a range of light availability. In general, we refer to a

'sun' (i.e. high light) environment as one with an open canopy, and a 'shade' (i.e. low light) environment as one with a closed canopy. Specifically, 'sun' environments included gaps with >10% canopy openness to completely open conditions; 'shade' environments included small gaps (<10% canopy openness) to completely closed forest understorey. When more than one 'shade' environment was considered in a study, we used the data corresponding with the lowest light availability. When different environments were assessed by a study, we avoided data from non-forest ecosystems (e.g. pasture), and opted instead for data from gaps or forest edges. Possible source of bias could arise from differences in the light environments used by different studies. A comparison of the canopy openness (i.e. the most common measure of light environment reported) quoted as 'shade' or as 'sun' in the different studies showed no significant difference amongst the three climates examined (results from one-way ANOVA for shade: $F_{2,18} = 0.66$, $p = 0.53$; sun: $F_{2,18} = 0.20$, $p = 0.82$; $n = 4$; SH temperate, $n = 5$; NH temperate, $n = 10$ tropical). This suggests that the light environments were overall comparable amongst climates. Most studies meeting our criteria used tree seedlings, saplings, and adults, whereas a limited number of the studies included used herbs or shrubs. We found some species (e.g. *Lindera benzoin*) and study sites (e.g. Barro Colorado) to be overrepresented relative to others (Table 1). When a study evaluated herbivory in more than one species, we included them as separate cases (i.e. replicates). When herbivory was measured on more than one date, we averaged across dates. Finally, when different treatments were applied in the different light environments (e.g. addition of fertilizer, herbivore exclusion) we only used the data from the controls. Our final list included 40 published studies and one unpublished study, covering 87 cases (i.e. comparisons) of intra-specific insect herbivory between contrasting light environments; 40 studies covered 70 plant species (a same species was sometimes used in two or more studies, Table 1) and one study covered six pooled species (Goodale et al. 2014); 38 studies used woody species (69 species) and three studies used herbaceous species (three species) (Liang and Stehlik 2009, Agrawal et al. 2012, Jones and Klemetti 2012) (Table 1). Geographically, the studies covered the temperate Northern Hemisphere (34° to 57°N, 32 cases), the temperate Southern Hemisphere (40° to 46°S, 12 cases), the subtropics (31°N to 33°S, one case which was treated as temperate) and the tropics (Northern and Southern Hemisphere) (20°N to 08°S, 42 cases) (Table 1). There were 23 cases of shade-intolerant species, 27 cases of semi-tolerant species, and 37 cases of shade-tolerant species (Table 1).

We extracted or estimated the following information from each selected study: name of plant species; level of herbivory for each light environment; light availability for each light environment; latitude; climate type (i.e. temperate, tropical); mean temperature for the first summer month (July for the Northern Hemisphere; January for the Southern Hemisphere); and ontogenetic stage of studied plants. Our study list included diverse measurements of herbivory

Table 1. List of studies and species (i.e. cases) included in our meta-analysis. In all cases insect herbivory was evaluated in two contrasting light environments (shade, canopy openness < 10%; sun, canopy openness > 10%). For each case, the source of data extraction for meta-analysis (i.e. text, table or figure), the latitude, the climate type, the mean temperature of the warmest month (estimated by DIVA-GIS, ver. 7.5.0.0), the shade tolerance (i: intolerant; m: semitolerant; t: tolerant), the leaf habit (D: deciduous; E: evergreen, H: herb), ontogeny, and light environments considered, are indicated.

Study	Source	Latitude	Climate	Summer T (°C)	Species	Tolerance	Habit	Ontogeny	Shade criteria	Sun criteria
Prather (2014)	Fig. 3, 4	18°19'00"N	tropical	22.5	<i>Miconia prasina</i>	i	E tree	sapling	< 10% CO	20-30% CO
Prather (2014)	Fig. 3, 4	18°19'00"N	tropical	22.5	<i>Miconia racemosa</i>	i	E tree	sapling	< 10% CO	20-30% CO
Prather (2014)	Fig. 3, 4	18°19'00"N	tropical	22.5	<i>Schefflera morototoni</i>	i	E tree	sapling	< 10% CO	20-30% CO
Prather (2014)	Fig. 3, 4	18°19'00"N	tropical	22.5	<i>Casearia arborea</i>	t	E tree	sapling	< 10% CO	20-30% CO
Prather (2014)	Fig. 3, 4	18°19'00"N	tropical	22.5	<i>Sloanea berteriana</i>	t	E tree	sapling	< 10% CO	20-30% CO
Prather (2014)	Fig. 3, 4	18°19'00"N	tropical	22.5	<i>Manilkara bidentata</i>	t	E tree	sapling	< 10% CO	20-30% CO
Angulo-Sandoval and Añel (2000)	Fig. 5	18°20'00"N	tropical	22.5	<i>Manilkara bidentata</i>	t	E tree	seedling	81.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$	737.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$
Lopez-Toledo et al. (2008)	Fig. 1d	16°07'12"N	tropical	27.2	<i>Brosimum alicastrum</i>	t	E tree	sapling	< 1.5 crown index	> 2.5 crown index ¹⁴
Gerhardt (1998)	Fig. 3 ²	10°51'00"N	tropical	25.0	<i>Swietenia macrophylla</i>	m	D tree	seedling	5–10% PAR	35–45% PAR
Gerhardt (1998)	Fig. 3 ²	10°51'00"N	tropical	25.0	<i>Cedrela odorata</i>	i	D tree	seedling	5–10% PAR	35–45% PAR
Letourneau and Dyer (1998)	Fig. 3	10°26'00"N	tropical	26.1	<i>Piper cenocladum</i>	t	E shrub	sapling	91.7% CC	83.3% CC
Dyer and Letourneau (1999)	Fig. 2b	10°26'00"N	tropical	26.1	<i>Piper cenocladum</i>	t	E shrub	sapling	> 96.6% cover	< 91.7% cover
de la Fuente and Marquis (1999)	Fig. 2	09°05'00"N	tropical	26.5	<i>Stryphnodendron microstachyum</i>	t	E tree	sapling	secondary forest	open pasture
Harrison (1987)	text	09°10'00"N	tropical	26.5	<i>Hybanthus prunifolius</i>	m	E shrub	sapling	understorey	gaps
Coley (1983)	Table 1	09°10'00"N	tropical	26.5	<i>Trichilia cipo</i>	m	E tree	sapling	understorey	100–800 m ² gaps
Pearson et al. (2003a)	Fig. 4 ³	09°10'00"N	tropical	26.5	<i>Miconia argentea</i>	m	D tree	seedling	6% CO ⁶	15% CO ¹⁹
Pearson et al. (2003a)	Fig. 4 ³	09°10'00"N	tropical	26.5	<i>Cecropia insignis</i>	m	E tree	seedling	6% CO ⁶	15% CO ¹⁹
Pearson et al. (2003a)	Fig. 4 ³	09°10'00"N	tropical	26.5	<i>Trema micrantha</i>	i	E tree	seedling	6% CO ⁶	15% CO ¹⁹
Richards and Coley (2008)	Table 2	09°05'00"N	tropical	26.5	<i>Hybanthus prunifolius</i>	m	E shrub	sapling	understorey	gap
Pearson et al. (2003b)	Fig. 3b	09°05'00"N	tropical	26.5	<i>Miconia argentea</i>	t	D tree	seedling	3.32% PAR	26.4% PAR
Pearson et al. (2003b)	Fig. 3b	09°05'00"N	tropical	26.5	<i>Cecropia insignis</i>	m	E tree	seedling	3.32% PAR	26.4% PAR
Pearson et al. (2003b)	Fig. 3b	09°05'00"N	tropical	26.5	<i>Luehea seemannii</i>	i	D tree	seedling	3.32% PAR	26.4% PAR
Pearson et al. (2003b)	Fig. 3b	09°05'00"N	tropical	26.5	<i>Trema micrantha</i>	i	E tree	seedling	3.32% PAR	26.4% PAR
Pearson et al. (2003b)	Fig. 3b	09°05'00"N	tropical	26.5	<i>Ochroma pyramidale</i>	i	E tree	seedling	3.32% PAR	26.4% PAR
Pearson et al. (2003b)	Fig. 3b	09°05'00"N	tropical	26.5	<i>Croton bilbergianus</i>	t	E tree	seedling	3.32% PAR	26.4% PAR
Goodale et al. (2014)	Table 2	06°23'23"N	tropical	22.9	<i>Dillenia triquetra</i> and five other	m	E tree	seedling	0.08 visual sky ¹⁰	0.36 visual sky ¹⁰
Norghauer and Newbery (2013)	Fig. 3 ⁴	05°17'09"N	tropical	25.0	<i>Microberlinia bisulcata</i>	i	D tree	seedling	5.53% CO ¹¹	7.69% CO ¹⁶
Norghauer and Newbery (2013)	Fig. 3 ⁴	05°17'09"N	tropical	25.0	<i>Tetraberlinia bifoliolata</i>	t	E tree	seedling	5.48% CO ¹²	8.23% CO ¹⁷

(Continued)

Table 1. Continued

Study	Source	Latitude	Climate	Summer		Species	Tolerance	Habit	Ontogeny	Shade criteria	Sun criteria
				T (°C)							
Norghauer and Newbery (2013)	Fig. 3 ⁴	05°17'09"N	tropical	25.0		<i>Tetralberlinia korupensis</i>	m	E tree	seedling	5.64% CO ¹³	9.21% CO ¹⁸
Eichhorn et al. (2010)	Fig. 1c, d	05°10'N	tropical	26.8		<i>Hopea nervosa</i>	t	D tree	seedling	understorey	400–600 m ² gap
Eichhorn et al. (2010)	Fig. 1c, d	05°10'N	tropical	26.8		<i>Parashorea tomentella</i>	t	D tree	seedling	understorey	400–600 m ² gap
Eichhorn et al. (2010)	Fig. 1c, d	05°10'N	tropical	26.8		<i>Shorea fallax</i>	t	E tree	seedling	understorey	400–600 m ² gap
Eichhorn et al. (2010)	Fig. 1c, d	05°10'N	tropical	26.8		<i>Shorea multiflora</i>	t	E tree	seedling	understorey	400–600 m ² gap
Eichhorn et al. (2010)	Fig. 1c, d	05°10'N	tropical	26.8		<i>Hopea beccariana</i>	t	E tree	seedling	understorey	400–600 m ² gap
Whitmore and Brown (1996)	Fig. 3b	04°54'00"N	tropical	24.8		<i>Hopea nervosa</i>	t	D tree	seedling	6% CO ⁷	26% CO ²²
Whitmore and Brown (1996)	Fig. 3b	04°54'00"N	tropical	24.8		<i>Parashorea malaanonan</i>	i	E tree	seedling	6% CO ⁷	26% CO ²²
Whitmore and Brown (1996)	Fig. 3b	04°54'00"N	tropical	24.8		<i>Shorea johorensis</i>	i	E tree	seedling	6% CO ⁷	26% CO ²²
Norghauer et al. (2008)	Fig. 3b	07°46'14"S	tropical	25.2		<i>Swietenia macrophylla</i>	m	D tree	seedling	7.1% CO ⁸	14.1% CO ²³
Benitez-Malvido et al. (2005)	Table 1	03°06'00"S	tropical	27.4		<i>Chrysophyllum pomiferum</i>	t	E tree	seedling	3.8% PAR	15.5% PAR
Benitez-Malvido et al. (2005)	Table 1	03°06'00"S	tropical	27.4		<i>Micropholis venulosa</i>	t	E tree	seedling	3.8% PAR	15.5% PAR
Benitez-Malvido et al. (2005)	Table 1	03°06'00"S	tropical	27.4		<i>Pouteria caimito</i>	t	E tree	seedling	3.8% PAR	75.6% PAR
Sinimbu et al. (2012)	Fig. 1h	02°24'00"S	tropical	27.0		<i>Inga paraensis</i>	i	E tree	sapling	<10% CO interior	>10% CO edge
Christie and Hochuli (2005)	Fig. 2	33°52'06"S	subtropical	21.5		<i>Angophora costata</i>	i	E tree	adult		
Löf et al. (2005)	Fig. 5	57°05'N	temp N	14.6		<i>Fagus sylvatica</i>	t	D tree	seedling	5% full light	20% full light
Löf et al. (2005)	Fig. 5	57°05'N	temp N	14.6		<i>Quercus robur</i>	m	D tree	seedling	5% full light	20% full light
Löf et al. (2005)	Fig. 5	57°05'N	temp N	14.6		<i>Tilia cordata</i>	m	D tree	seedling	5% full light	20% full light
Löf et al. (2005)	Fig. 5	57°05'N	temp N	14.6		<i>Acer platanoides</i>	t	D tree	seedling	5% full light	20% full light
Löf et al. (2005)	Fig. 5	57°05'N	temp N	14.6		<i>Fraxinus excelsior</i>	m	D tree	seedling	5% full light	20% full light
Löf et al. (2005)	Fig. 5	57°05'N	temp N	14.6		<i>Prunus avium</i>	i	D tree	seedling	5% full light	20% full light
Löf et al. (2005)	Fig. 5	57°05'N	temp N	14.6		<i>Picea abies</i>	t	E tree	seedling	5% full light	20% full light
Karolewski et al. (2013)	Fig. 2	52°33'00"N	temp N	16.5		<i>Sambucus nigra</i>	m	D tree	adult	understorey ⁹	open ²¹
Karolewski et al. (2013)	Fig. 2	52°33'00"N	temp N	16.5		<i>Cornus sanguinea</i>	m	D tree	adult	understorey ⁹	open ²¹
Karolewski et al. (2013)	Fig. 2	52°33'00"N	temp N	16.5		<i>Frangula alnus</i>	m	D tree	adult	understorey ⁹	open ²¹
Karolewski et al. (2013)	Fig. 2	52°33'00"N	temp N	16.5		<i>Corylus avellana</i>	t	D tree	adult	understorey ⁹	open ²¹

(Continued)

Table 1. Continued

Study	Source	Latitude	Climate	Summer		Species	Tolerance	Habit	Ontogeny	Shade criteria	Sun criteria
				T (°C)							
Karolewski et al. (2013)	Fig. 2	52°33'00"N	temp N	16.5		<i>Prunus serotina</i>	i	D tree	adult	understorey ⁹	open ²¹
Karolewski et al. (2013)	Fig. 2	52°33'00"N	temp N	16.5		<i>Prunus padus</i>	m	D tree	adult	understorey ⁹	open ²¹
McGeoch and Gaston (2000)	Table 3	53°20'31"N	temp N	14.2		<i>Ilex aquifolium</i>	m	E tree	adult	interior	edge
Liang and Stehlik (2009)	Fig. 2	44°01'46"N	temperate N	24.4		<i>Asarum canadense</i>	t	H	adult	>91% CC	<85% CC
Agrawal et al. (2012)	Fig. 1d	42°27'27"N	temperate N	20.5		<i>Asclepias syriaca</i>	m	H	adult	168 $\mu\text{mol m}^{-2} \text{s}^{-1}$	1784 $\mu\text{mol m}^{-2} \text{s}^{-1}$
Niesenbaum and Kluger (2006)	Fig. 2A	40°40'13"N	temperate N	19.5		<i>Lindera benzoin</i>	t	D shrub	adult	14.39 $\mu\text{mol m}^{-2} \text{s}^{-1}$	214.08 $\mu\text{mol m}^{-2} \text{s}^{-1}$
Niesenbaum (1992)	Table 2	40°40'13"N	temperate N	19.5		<i>Lindera benzoin</i>	t	D shrub	adult	0.86% full light ¹⁵	19.84% full light ²⁴
Muth et al. (2008)	Fig. 1	40°40'13"N	temperate N	19.5		<i>Lindera benzoin</i>	t	D shrub	adult	48 $\mu\text{mol m}^{-2} \text{s}^{-1}$	658.30 $\mu\text{mol m}^{-2} \text{s}^{-1}$
Lieurance and Cipollini (2012)	Fig. 1a, c	40°1'-39°3'N	temperate N	20.7		<i>Lonicera maackii</i>	m	D shrub	adult	interior	edge
Jones and Klemetti (2012)	Fig. 2	41°57'59"N	temperate N	14.4		<i>Trollius laxus</i>	i	H	adult	<150 $\mu\text{mol m}^{-2} \text{s}^{-1}$	> 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$
Arrieta and Suárez (2005)	Fig. 4 ⁵	41°57'59"N	temperate N	14.4		<i>Ilex aquifolium</i>	m	E tree	seedling	0.70% PPFD	46.59% PPFD
Stoepler and Rehill (2012)	Fig. 3 ⁶	39°15'9"N	temperate N	21.1		<i>Quercus alba</i>	m	D tree	sapling	2.4% CO	57.9% CO
Lincoln and Mooney (1984)	Fig. 1	37°24'N	temperate N	20.0		<i>Diplacus aurantiacus</i>	m	D shrub	adult	<15 $\text{mol m}^{-2} \text{d}^{-1}$	>40 $\text{mol m}^{-2} \text{d}^{-1}$
Shure and Wilson (1993)	Fig. 6	35°12'43"N	temperate N	19.3		<i>Robinia pseudoacacia</i>	i	D tree	sapling	understorey	0.08 ha's gap
Shure and Wilson (1993)	Fig. 6	35°12'43"N	temperate N	19.3		<i>Cornus florida</i>	t	D tree	sapling	understorey	0.08 ha's gap
Shure and Wilson (1993)	Fig. 6	35°12'43"N	temperate N	19.3		<i>Liriodendron tulipifera</i>	i	D tree	sapling	understorey	0.08 ha's gap
Shure and Wilson (1993)	Fig. 6	35°12'43"N	temperate N	19.3		<i>Acer rubrum</i>	t	D tree	sapling	understorey	0.08 ha's gap
Hunter and Forkner (1999)	Fig. 5a	35°N	temperate N	19.3		<i>Acer rubrum</i>	t	D tree	sapling	interior	0.2-0.4 ha open area
Hunter and Forkner (1999)	Fig. 5b	35°N	temperate N	19.3		<i>Quercus rubra</i>	i	D tree	sapling	interior	0.2-0.4 ha open area
Dudt and Shure (1994)	Fig 6.	34°41'37"N	temperate N	22.1		<i>Liriodendron tulipifera</i>	i	D tree	seedling	6% full light	80 m ² gap ^{2,5}
Dudt and Shure (1994)	Fig 6.	34°41'37"N	temperate N	22.1		<i>Cornus florida</i>	t	D tree	seedling	6% full light	80 m ² gap ^{2,5}
Piper, F. unpubl.		46°29'51"S	temperate S	12.9		<i>Amomyrtus luma</i>	t	E tree	seedling	< 7 % CO	> 10% CO
Piper, F. unpubl.		46°29'51"S	temperate S	12.9		<i>Drymis winteri</i>	m	E tree	seedling	< 7 % CO	> 10% CO

(Continued)

Table 1. Continued

Study	Source	Latitude	Climate	Summer T (°C)	Species	Tolerance	Habit	Ontogeny	Shade criteria	Sun criteria
Piper, F. unpubl.		45°27'07"S	temperate S	11.7	<i>Aristotelia chilensis</i>	i	E tree	seedling	< 7 % CO	> 10% CO
Piper, F. unpubl.		45°27'07"S	temperate S	11.7	<i>Amomyrtus luma</i>	t	E tree	seedling	< 7 % CO	> 10% CO
Piper, F. unpubl.		45°27'07"S	temperate S	11.7	<i>Azara lanceolata</i>	m	E tree	seedling	< 7 % CO	> 10% CO
Piper, F. unpubl.		45°27'07"S	temperate S	11.7	<i>Luma apiculata</i>	t	E tree	seedling	< 7 % CO	> 10% CO
Bach and Kelly (2004)	text	43°09'S	temperate S	11.0	<i>Alepis flavida</i>	t	E shrub	adult	interior	edge
Chacón and Armeño (2006)	Fig. 3	41°53'00"S	temperate S	12.4	<i>Drimys winteri</i>	m	E tree	seedling	1% CO	11.5% CO
Chacón and Armeño (2006)	Fig. 3	41°53'00"S	temperate S	12.4	<i>Cevuina avellana</i>	m	E tree	seedling	1% CO	11.5% CO
Piper, F. unpubl.		41°35'00"S	temperate S	15.2	<i>Amomyrtus meli</i>	t	E tree	sapling	< 7 % CO	> 10% CO
Salgado-Luarte and Gianoli (2010)	Fig. 1A	40°39'00"S	temperate S	15.2	<i>Embothrium coccineum</i>	i	E tree	seedling	5% full light	67% full light
Salgado-Luarte and Gianoli (2012)	Fig. 1A	40°39'00"S	temperate S	15.2	<i>Aristotelia chilensis</i>	i	E tree	seedling	5.1% CO	25.6% CO

¹ mean temperature of July for the Northern Hemisphere and January for Southern Hemisphere

² average for two forests (deciduous and semievergreen); Th0Tr0 only

³ outside exclosures only

^{4,6} controls only

⁵ 1997s cohort; edge versus closed holly woodland

⁶ 0.2 mol m⁻² day⁻¹; 2.83% PAR, 0.13 GSF

⁷ 1 mol m⁻² day⁻³

⁸ 4.5 mol m⁻² day⁻¹

⁹ under a canopy of *Pinus sylvestris* with admixture of *Quercus robur*, *Fagus sylvatica*, *Carpinus betulus* and *Ulmus laevis*

¹⁰ proportion at 180°

¹¹ 0.59% PPF

¹² 0.73% PPF

¹³ 1.10% PPF

¹⁴ gaps >200 m²

¹⁵ 9.18 μmol m⁻² s⁻¹

¹⁶ 5.36% PPF

¹⁷ 5.39% PPF

¹⁸ 6.04% PPF

¹⁹ 8 mol m⁻² day⁻¹, 26.9% PAR, 0.27 GSF

²⁰ 0.269 GSF

²¹ along wide forest roads or in forest gaps

²² 19 mol m⁻² day⁻¹

²³ 12.8 mol m⁻² day⁻¹

²⁴ 115.68 mmol m⁻² s⁻¹

²⁵ 24% full light

For Prather (2014) "shade" was "trim, no debris", and "sun" was "no trim, no debris"

(e.g. herbivory index, % leaf area removed), mostly corresponding to folivory (Supplementary material Appendix 1 Table A1). The mean values for herbivory, standard deviations, confidence intervals or standard errors (for standard deviation calculation), and sample size were extracted for each light environment from the text, the tables or the figures, in the latter case using the software TechDig (ver. 2.0, Ronald B. Jones). When the results did not include the standard deviations, confidence intervals or standard errors, we attempted to contact the authors for the information; two studies had to be omitted because of no response. When the sampling unit was not clearly stated, we used the largest scale sampling unit (i.e. sites over plots; plots over plants; plants over leaves) and in some cases averaged values from smaller scales to generate larger scale values (e.g. leaves to plant). Here, we assumed independence among sample units. Some studies considered different individuals of a same plot, or different leaves of same plants, as replicates. In these cases, we averaged herbivory values of plants of a same plot or leaves of a same plant and considered it as a replicate. Latitude was recorded using the geographic coordinates reported in the study or Google Earth (ver. 7.1.5.1557) when they were not provided. The mean temperature for the first summer month was estimated for each study site using Worldclim (ver. 1, 30 sec ESRI data bases) (Hijmans et al. 2005) and DIVA-GIS software (ver. 7.5.0.0). We used the first summer month (i.e. the warmest) for our temperature measurement because it is generally the period of seedling establishment, the maximum expansion rate of new leaves, and the maximum rate of herbivory in temperate forests (Coley and Aide 1991, Lowman 1992, Carus 2009). More importantly, this is usually the month for which herbivory data were reported in most studies.

Leaf habit (deciduous or evergreen) and shade tolerance (shade-tolerant, semi-tolerant, shade-intolerant) of the studied plant species were obtained from the original publications and from web databases. The latter included The Plant List (< www.theplantlist.org/ >), Encyclopedia of Life (< <http://eol.org/> >), Global Species (< www.globalspecies.org/ >), Integrated Taxonomic Information System (< www.itis.gov/ >), and Global Biodiversity Information Facility (< www.gbif.org/ >).

Data analyses

For each case, we quantified the difference in herbivory damage between shade and sun environments as the effect size. An effect size is a standardized measure of the magnitude of the observed effect. Thus, effect sizes across studies that have measured herbivory in diverse ways and in diverse units or scales, can be directly analysed (Field and Gillett 2010). We chose the standardized mean difference, specifically ‘Hedges’s g ’, as a metric of the effect size, defined as the difference between the means of two groups divided by their pooled standard deviation (Gurevitch and Hedges 1993). This number is then multiplied by a correction factor J , to correct for small-sample bias. In our case, ‘sun’ herbivory was considered

as the ‘experimental group’ and ‘shade’ herbivory as the ‘control group’. Thus, a positive effect size means that herbivory is higher in sun than in shade, while a negative effect size means the opposite. The effect size was calculated as:

$$d_{ij} = \left(X_{ij}^{sun} - X_{ij}^{shade} \right) / S_{ij} \times J$$

where d is calculated for the j th study in the i th study class; X_{ij}^{sun} is the mean of the sun group; X_{ij}^{shade} is the mean of the shade group; S_{ij} is the pooled standard deviation of the sun and shade groups; and J is a correction factor for small sample sizes. Our analyses did not correct a priori for publication bias because most of the selected studies did not address the difference in herbivory between light environments as a target research question. More often they treated the effect of light environment on the growth or abundance of plants, the performance of insect herbivores, or the interaction of light environment with a particular treatment (e.g. fertilization) on the performance or abundance of herbivores.

We first tested the effect of light environment on insect herbivory on a global scale (i.e. across climates), by comparing the effect sizes between ‘sun’ and ‘shade’, using fully random-effects analyses. Then, climate type and shade tolerance were treated as moderators and their effects were examined using mixed effects analysis. Climate was tested based on the following sub-groups: northern temperate, southern temperate and tropical (the only subtropical study was treated as SH temperate). Shade tolerance was tested based on the following sub-groups: shade-tolerant, shade-intolerant, shade semi-tolerant. A random effects model was used to combine studies within each subgroup (i.e. climate or shade tolerance category), and a fixed effect model was used to combine subgroups and yield the overall effect. The study-to-study variance (tau-squared) was assumed to be the same for all subgroups – this value was computed within subgroups and then pooled across subgroups. Mixed-effects models are more appropriate than fixed-effects models for making inferences that generalize beyond the studies included in the meta-analysis (Field and Gillett 2010). They assume that the average effect size in a population varies randomly from study to study: studies in a meta-analysis are made up of populations with different average effect sizes (Field and Gillett 2010). Mixed-effect models consider two sources of error: 1) error created by sampling studies from a population, and 2) error created by sampling individual populations from a universe of populations (Field and Gillett 2010).

Latitude and temperature were also considered as moderators and their effects evaluated by meta-regression. Latitude was examined either distinguishing or not between hemispheres (i.e. using negative sign for the Southern Hemisphere and positive sign for the norther hemisphere, or using always positive values, respectively). Meta-regression under random-effect model was also used to assess the combined impact of climate, latitude, temperature and shade tolerance. All analyses were performed with comprehensive meta-analysis software (ver. 3.3.070, 2014).

Results

Globally, there were 19 cases of higher insect herbivory in the sun, 10 cases of higher herbivory in the shade, and 58 cases of no difference between contrasting light environments (Supplementary material Appendix 1 Table A2). The mean effect size of the complete data set was positive and just significantly different from zero ($d=0.221$, $SE=0.113$, 95% $CI=0.000-0.443$, $n=87$; Z -value = 1.957, p -value = 0.050), indicating that insect herbivory at a global scale was marginally but significantly higher in sun than in shade (Fig. 2). There was no significant overall effect of climate type on the herbivory at sun versus shade (Q -value = 4.132, $df=2$, $p=0.127$). However, when climates were analysed separately (i.e. as subgroups), herbivory in the tropics was significantly higher in the sun than in the shade (i.e. positive effect size) ($d=0.413$, $SE=0.162$; 95% $CI=0.026-0.097$, $n=42$; $Z=2.558$, $p=0.011$) (Fig. 2). In both northern and southern temperate zones, insect herbivory was similar between

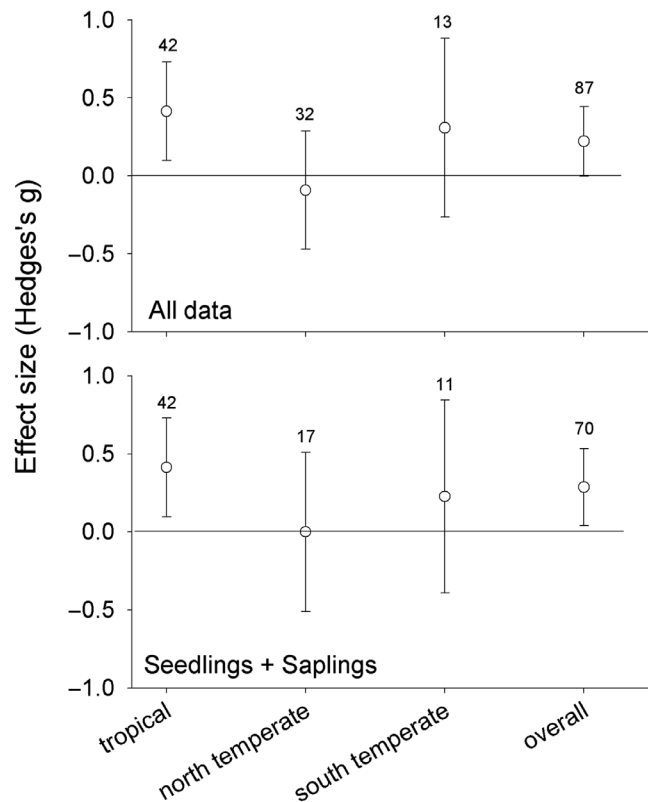


Figure 2. Mean and 95% confidence intervals for the effect sizes of light environment (sun versus shade, Table 1) on insect herbivory (weighted standardized mean, Hedges's g) for all study cases (i.e. a study \times species' combination; $n=87$), study cases of tropical forests ($n=42$), study cases of north temperate forests ($n=32$), and study cases of south temperate forests ($n=13$). Positive values indicate preference for sunny over shady environments. Upper panel shows results for the complete data set, including seedlings, saplings and adults; lower panel shows results for seedlings and saplings (i.e. subgroup 'adults' excluded).

light environments (Supplementary material Appendix 1 Table A2, Fig. 2).

Most studies were conducted on seedlings or saplings, with a lower proportion of studies conducted on adult plants. The latter, however, represented ca 50% of the case studies in Northern Hemisphere temperate forests, but 0% of the tropical cases. To control for possible ontogenetic effects on our results, we re-ran our analyses excluding adult plants. The mean effect size in this case was positive and significantly different from zero ($d=0.287$, $SE=0.123$, 95% $CI=0.045-0.529$, $n=70$; test of the null: $Z=2.326$, $p=0.020$). Also, climate type had no significant overall effect on herbivory in sun versus shade ($Q=1.860$, $df=2$, $p=0.395$), but herbivory was higher in sun than in shade in the tropics ($d=0.413$, $SE=0.162$; 95% $CI=0.096-0.731$, $n=42$; $Z=2.552$, $p=0.011$) and similar between light environments for the other biomes (Fig. 2).

Globally, species shade tolerance had no effect on the relative levels of herbivory in sun and shade environments ($Q=1.405$, $df=2$, $p=0.495$). However, as a group, shade-intolerant species suffered more herbivory in the sun than in the shade ($d=0.428$, $SE=0.216$, 95% $CI=0.004-0.852$, $n=23$; $Z=1.979$, $p=0.049$), while herbivory rates suffered by semi-tolerant and shade-tolerant species did not differ between light environments (Fig. 3).

Variation in effect sizes was not explained by temperature or latitude (Table 2). Models including different combinations of moderators also failed to explain the variation in effect sizes (Table 2). However, 'climate' had a marginally significant effect in model 8. Temperature and latitude, and different combinations of moderators, also failed to explain the variation in effect sizes for studies considering seedlings and saplings only (Table 3). The moderator 'climate' had a significant effect in two models (model 5 and 8, Table 3).

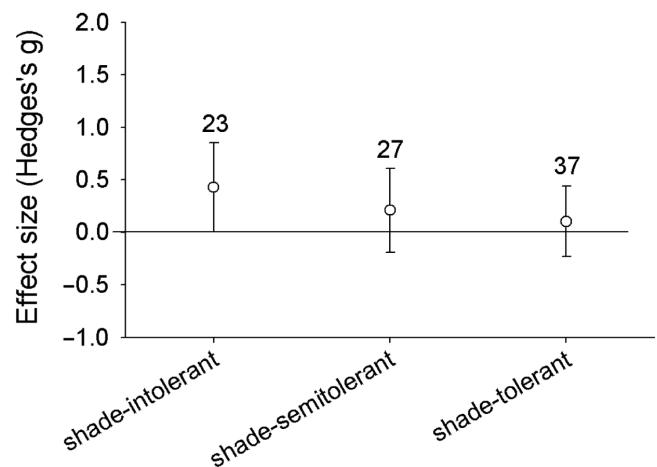


Figure 3. Mean and 95% confidence intervals for the effect sizes of light environment (sun versus shade, Table 1) on insect herbivory (weighted standardized mean, Hedges's g) for case studies conducted in shade-intolerant species ($n=23$), shade semi-tolerant ($n=27$) and shade-tolerant ($n=37$). Negative values indicate preference for sunny over shady environments.

Table 2. Effects of different moderators on the effect sizes of insect herbivory in sun versus shade for all case studies (Table 1), examined by meta-regression. Tau² (variance of true effect sizes) and I² (between-study variance, i.e. that can be potentially explained by additional study-level covariates) indicate the variance that is not explained by the model (goodness of fit).

Model	Moderators	Q-value	df	p	R ²	Tau ²	I ²	Details
1	Temperature	0.72	1	0.396	0.00	0.86	86%	
2	Climate type	4.13	2	0.127	0.00	0.86	85%	
3	Latitude 1	1.45	1	0.228	0.00	0.86	85%	
4	Latitude 2	2.41	1	0.121	0.03	0.81	85%	
5	Temperature Climate type	4.23	2	0.121	0.02	0.83	85%	Coef. = -0.05 (0.04), p=0.248 Coef. = 0.81 (0.43), p=0.060
6	Temperature Latitude 2	4.30	2	0.117	0.12	0.74	83%	Coef. = -0.06 (0.05), p=0.185 Coef. = -0.25 (0.01), p=0.060
7	Temperature Climate type Latitude 2	4.84	3	0.184	0.11	0.74	84%	Coef. = -0.06 (0.05), p=0.181 Coef. = 0.50 (0.65), p=0.445 Coef. = -0.01 (0.02), p=0.536
8	Temperature Climate type Shade tol.	6.10	4	0.182	0.06	0.78	84%	Coef. = -0.05 (0.04), p=0.237 Coef. = 0.83 (0.43), p=0.051 Q= 1.76, df=2, p=0.415
9	Temperature Climate type Shade tol Latitude 2	6.52	5	0.259	0.10	0.75	83%	Coef. = -0.06 (0.05); p=0.204 Coef. = 0.58 (0.66); p=0.38 Q= 1.70, df=2, p=0.43 Coef. = -0.01 (0.02), p=0.63

Latitude 1 was computed always positive, i.e. not distinguishing between hemispheres; Latitude 2 included positive and negative values for Northern and Southern Hemispheres, respectively. Model 2 considered three subgroups in *Climate type*, ('tropical', 'NH temperate', 'SH temperate'); models 5, 7, 8 and 9 considered two subgroups ('temperate' and 'tropical').

When models were run separately for each climate type, we found a negative effect of temperature in tropical climates, indicating that the effect of gaps on herbivory decreases with increasing temperature (Table 4). In temperate forests, however, neither temperature nor latitude explained the variation in effect size.

Discussion

Our meta-analysis did not support our first hypothesis, that temperature limitation is the primary control on patterns of insect herbivory. Assuming that in temperate regions temperatures are suboptimal for most insects (Frazier et al. 2006,

Table 3. Effects of different moderators on the effect sizes of insect herbivory in sun versus shade for case studies including seedlings and saplings only (Table 1), examined by meta-regression (n=70, Table 1). Tau² (variance of true effect sizes) and I² (between-study variance, i.e. that can be potentially explained by additional study-level covariates) indicate the variance that is not explained by the model (goodness of fit).

Model	Moderators	Q-value	df	p	R ²	Tau ²	I ²	Details
1	Temperature	0.14	1	0.710	0.00	0.85	87%	
2	Climate type	1.86	2	0.395	0.00	0.86	86%	
3	Latitude 1	0.08	1	0.782	0.00	0.86	85%	
4	Latitude 2	0.77	1	0.379	0.00	0.81	86%	
5	Temperature Climate type	4.56	2	0.102	0.01	0.80	86%	Coef. = -0.09 (0.05), p=0.086 Coef. = 1.19 (0.56), p=0.035
6	Temperature Latitude 2	2.92	2	0.232	0.17	0.68	83%	Coef. = -0.09 (0.06), p=0.153 Coef. = -0.03 (0.02), p=0.096
7	Temperature Climate type Latitude 2	5.10	3	0.165	0.14	0.70	84%	Coef. = -0.10 (0.06), p=0.110 Coef. = 1.05 (0.70), p=0.133 Coef. = -0.01 (0.02), p=0.765
8	Temperature Climate type Shade tol.	6.49	4	0.165	0.14	0.70	84%	Coef. = -0.09 (0.05), p=0.071 Coef. = 1.23 (0.55), p=0.026 Q= 1.72, df=2, p=0.420
9	Temperature Climate type Shade tol Latitude 2	6.84	5	0.232	0.14	0.70	83%	Coef. = -0.09 (0.06); p=0.128 Coef. = 0.58 (0.66); p=0.38 Q= 1.78, df=2, p=0.41 Coef. = -0.00 (0.02), p=0.91

Latitude 1 was computed always positive, i.e. not distinguishing between hemispheres; Latitude 2 included positive and negative values for Northern and Southern Hemispheres, respectively. Model 2 considered three subgroups in *Climate type*, ('tropical', 'NH temperate', 'SH temperate'); models 5, 7, 8 and 9 considered two subgroups ('temperate' and 'tropical').

Table 4. Effects of temperature, latitude, and the combination of both on the effect sizes of insect herbivory in sun versus shade in tropical (n=42, Table 1) and temperate forests (n=28, Table 1), examined by meta-regression. Only case studies including seedlings and saplings were analyzed. Tau² (variance of true effect sizes) and I² (between-study variance, i.e. that can be potentially explained by additional study-level covariates) indicate the variance that is not explained by the model (goodness of fit).

Model	Moderators	Q-value	df	p	R ²	Tau ²	I ²	Details
tropical								
1	Temperature	2.31	1	0.129	0.07	0.98	89%	
2	Latitude	0.13	1	0.718	0.02	0.99	72%	
3	Temperature Latitude	4.03	2	0.133	0.30	0.75	85%	Coef. = -0.25 (0.13), p=0.048 Coef. = -0.04 (0.04), p=0.304
temperate								
1	Temperature	1.34	1	0.247	0.00	0.39	72%	
2	Latitude	0.78	1	0.377	0.00	0.39	72%	
3	Temperature Latitude	1.37	2	0.503	0.00	0.40	72%	Coef. = 0.06 (0.06), p=0.279 Coef. = -0.00 (0.00), p=0.789

Deutsch et al. 2008, Huey 2010), and in view of a general positive correlation between light availability and temperature (Andrew et al. 2012), we had predicted that the relative importance of understorey herbivory should decrease with latitude, with insect herbivory being higher in gaps than in understoreys in temperate forests – especially in the oceanic climates of the Southern Hemisphere (Fig. 1). Contrary to our prediction, our meta-analysis found that insect herbivory was lower in the understorey than in gaps in general, and in tropical forests in particular (Fig. 2). The fact that preferential carbon allocation to storage in late-successional species is more characteristic of tropical than of temperate forests (Kitajima 1994, Canham et al. 1999, Lusk and Piper 2007, Myers and Kitajima 2007, Poorter and Kitajima 2007, Piper 2015) is therefore unlikely to be explained by differential herbivore responses to light availability gradients in tropical versus temperate forests. Although the low opportunity cost of allocation to storage in shaded understoreys has been emphasized (Kobe 1997), it is unclear why similar patterns have not consistently been observed in shade-tolerant species of temperate forests (Canham et al. 1999, Lusk and Piper 2007). Interestingly, one aspect of our first hypothesis did receive support from one of our models: a negative impact of temperature on gap herbivory was found in tropical forests (Table 4). This result is consistent with insect avoidance of stress by radiative heating at high temperatures.

Meta-analysis supported our second hypothesis, that light environment influences insect herbivore pressure on plants through its effect on resource availability to herbivores (Richards and Coley 2008). However, although this effect was supported at a global scale, this result was entirely driven by strong patterns in tropical forests, the best-represented climate type in our compilation (Fig. 2, Table 1). Here, we found that the insect herbivory was significantly higher in sun than in shade. Higher herbivory in sun than in shade of tropical forests could reflect both greater plant growth and biomass in gaps (Bazzaz 1979), but also higher nutritional and energetic status of foliage. For instance, Richards and Coley (2008) found that the lepidopteran larva *Zunacetha annulata* feeding on sun leaves of its host plant *Hybanthus prunifolius*, ate 22 percent less leaf area, grew 25 percent faster, and had higher

pupal weights than larvae feeding on shade leaves. Although Richards and Coley (2008) found higher nitrogen concentration in shade leaves, both soil nitrogen mineralization and leaf nutrient status have been found to positively relate to light availability (Osier and Jennings 2007, Takafumi et al. 2010; but see Lusk and Reich 2000). The effect of gaps on plant growth and biomass could be more accentuated in the tropics, where understorey to gap-centre gradients of light availability are most pronounced (Ricklefs 1977, Lusk et al. 2011). In addition, faster leaf turnover in gaps than in the understorey could make gaps richer in availability of young leaves (Lowman 1992, Vincent 2006, Lusk and Corcuera 2011), which generally are more palatable than old leaves (Coley and Barone 1996). The strong effect of gaps on herbivory of shade-intolerant species (Fig. 3) is also consistent with our second (resource limitation) hypothesis. While shade-intolerant species exhibit significant biomass increments in response to increasing light availability, shade-tolerant species are less responsive (Bazzaz 1979, King 1994, Kitajima 1994). Thus, the nutritional benefit obtained by herbivores in gaps is expected to be much higher for shade-intolerant than for shade-tolerant species.

Higher herbivory in gaps could also occur if gaps attract fewer natural enemies of insect herbivores than the understorey. In a Puerto Rican montane tropical forest, the density of frogs that prey on a wide range of invertebrates was strongly reduced by experimental canopy opening (Klawinski et al. 2014). On the other hand, evidence from both tropical and temperate forests indicates that the impact of parasitism and predation on herbivores may be actually higher in gaps than in the neighbouring understorey (Harrison 1987, Richards and Coley 2007, 2008, Stoepler and Lill 2013). However, Richards and Coley (2007) reported that insect herbivory rates in tropical forests were higher in gaps than in understoreys, despite higher predator abundance in gaps. Spatial variation in pressure from natural enemies of insect herbivores therefore seems unlikely to explain higher rates of leaf damage in gaps than in understoreys.

Our findings have bearing on the long-standing question about latitudinal patterns of herbivory (MacArthur 1969, Coley and Aide 1991). In most studies examining

this question, herbivory has been evaluated under a similar light environment for the whole latitudinal range considered, attempting to standardize factors other than latitude. Our findings imply that patterns revealed by latitudinal comparisons of herbivory rates will depend on the light environment chosen by researchers. Regional differences in the effect of light environment on insect herbivory rates could account for the inconsistency among studies analysing latitudinal patterns of insect herbivory (Coley and Aide 1991, del-Val and Armesto 2010, Moles et al. 2011, Zhang et al. 2016).

Conclusions

Our study did not support the hypothesis that understory insect herbivory in temperate forests (particularly in the Southern Hemisphere), is limited by low temperature. In contrast, our results are consistent with the hypothesis that the forest understory limits resource availability for herbivores, especially in the tropics. The evidence that insect herbivory rates overall were higher in gaps than in understories suggests the selective importance of insect herbivory in forest understories may have been over-estimated. Our finding of latitudinal moderation of the effect of light environment on insect herbivory indicates that future investigations of latitudinal trends in herbivory should consider multiple light environments.

Acknowledgments – We thank Lee Dyer and Chelse Prather for providing information on their studies, Julian Norghauer for providing SE data, Ernesto Gianoli for inspiring discussion on the topic and Mikhail Kozlov for helpful and constructive comments.

Funding – We thank Fondecyt (grants 11121175 and 1160330) and the Environmental Research Inst. (Univ. of Waikato) for financial support.

References

- Agrawal, A. A. et al. 2012. Attenuation of the jasmonate burst, plant defensive traits, and resistance to specialist monarch caterpillars on shaded common milkweed (*Asclepias syriaca*). – *J. Chem. Ecol.* 38: 893–901.
- Andrew, N. R. et al. 2012. Insect herbivory along environmental gradients. – *Open J. Ecol.* 2: 202–213.
- Angulo-Sandoval, P. and Aide, T. M. 2000. Effect of plant density and light availability on leaf damage in *Manilkara bidentata* (Sapotaceae). – *J. Trop. Ecol.* 16: 447–464.
- Arrieta, S. and Suárez, F. 2005. Spatial patterns of seedling emergence and survival as a critical phase in holly (*Ilex aquifolium* L.) woodland recruitment in central Spain. – *For. Ecol. Manage.* 205: 267–282.
- Augspurger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. – *J. Ecol.* 72: 777–795.
- Bach, K. E. and Kelly, D. 2004. Effects of forest edges on herbivory in a New Zealand mistletoe, *Alepis flavida*. – *N. Z. J. Ecol.* 28: 195–206.
- Bazzaz, F. A. 1979. The physiological ecology of plant succession. – *Annu. Rev. Ecol. Syst.* 10: 351–371.
- Benitez-Malvido, J. et al. 2005. Responses of seedling transplants to environmental variations in contrasting habitats of central Amazonia. – *J. Trop. Ecol.* 21: 397–406.
- Canham, C. D. et al. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. – *Oecologia* 121: 1–11.
- Carus, S. 2009. Effects of defoliation caused by the processionary moth on growth of Crimean pines in western Turkey. – *Phytoparasitica* 37: 105–114.
- Chacón, P. and Armesto, J. 2006. Do carbon-based defences reduce foliar damage? Habitat-related effects on tree seedling performance in a temperate rainforest of Chiloé Island, Chile. – *Oecologia* 146: 555–565.
- Christie, F. J. and Hochuli, D. F. 2005. Elevated levels of herbivory in urban landscapes: are declines in tree health more than an edge effect?. – *Ecol. Soc.* 10: 10.
- Coley, P. D. 1983. Intraspecific variation in herbivory on two tropical tree species. – *Ecology* 64: 426–433.
- Coley, P. D. and Aide, M. T. 1991. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. – In: Price, P. W. et al. (eds), *Plant–animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley-Interscience, pp. 25–49.
- Coley, P. D. and Barone, J. A. 1996. Herbivory and plant defenses in tropical forests. – *Annu. Rev. Ecol. Syst.* 27: 305–335.
- Coley, P. D. et al. 1985. Resource availability and plant antiherbivore defense. – *Science* 230: 895–899.
- de la Fuente, M. A. S. and Marquis, R. J. 1999. The role of attended extrafloral nectaries in the protection and benefit of a Neotropical rainforest tree. – *Oecologia* 118: 192–202.
- del-Val, E. and Armesto, J. J. 2010. Seedling mortality and herbivory damage in subtropical and temperate populations: testing the hypothesis of higher herbivore pressure toward the tropics. – *Biotropica* 42: 174–179.
- Deutsch, C. A. et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. – *Proc. Natl Acad. Sci. USA* 105: 6668–6672.
- Dudt, J. F. and Shure, D. J. 1994. The influence of light and nutrients on foliar phenolics and insect herbivory. – *Ecology* 75: 86–98.
- Dyer, L. A. and Letourneau, D. K. 1999. Relative strengths of top–down and bottom–up forces in a tropical forest community. – *Oecologia* 119: 265–274.
- Eichhorn, M. P. et al. 2010. Herbivory of tropical rain forest tree seedlings correlates with future mortality. – *Ecology* 91: 1092–1101.
- Field, A. P. and Gillett, R. 2010. How to do a meta-analysis. – *Br. J. Math. Stat. Psychol.* 63: 665–694.
- Frazier, M. R. et al. 2006. Thermodynamics constrains the evolution of insect population growth rates: “warmer is better”. – *Am. Nat.* 168: 512–520.
- Garibaldi, L. A. et al. 2011. Latitudinal decrease in folivory within *Nothofagus pumilio* forests: dual effect of climate on insect density and leaf traits? – *Global Ecol. Biogeogr.* 20: 609–619.
- Gerhardt, K. 1998. Leaf defoliation of tropical dry forest tree seedlings – implications for survival and growth. – *Trees-Structure Funct.* 13: 88–95.
- Goodale, U. M. et al. 2014. Differences in survival and growth among tropical rain forest pioneer tree seedlings in relation to canopy openness and herbivory. – *Biotropica* 46: 183–193.

- Guerra, P. et al. 2010. Explaining differential herbivory in sun and shade: the case of *Aristotelia chilensis* saplings. – *Arthropod-Plant Interactions* 4: 229–235.
- Gurevitch, J. and Hedges, L. V. 1993. Meta-analysis: combining the results of independent experiments. – In: Scheiner, S. and Gurevitch, J. (eds), *Design and analysis of ecological experiments*. Chapman and Hall.
- Harrison, S. 1987. Treefall gaps versus forest understory as environments for a defoliating moth on a tropical forest shrub. – *Oecologia* 72: 65–68.
- Heinrich, B. 1995. Insect thermoregulation. – *Endeavour* 19: 28–33.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- Huey, R. B. 2010. Evolutionary physiology of insect thermal adaptation to cold environments. – In: Denlinger, D. L. and Lee, R. J. (eds), *Low temperature biology of insects*. Cambridge Univ. Press.
- Hunter, M. D. and Forkner, R. E. 1999. Hurricane damage influences foliar polyphenolics and subsequent herbivory on surviving trees. – *Ecology* 80: 2676–2682.
- Jones, K. N. and Klemetti, S. M. 2012. Managing marginal populations of the rare wetland plant *Trollius laxus* Salisbury (spreading globeflower): consideration of light levels, herbivory and pollination. – *Northeastern Nat.* 19: 267–278.
- Karolewski, P. et al. 2013. Season and light affect constitutive defenses of understory shrub species against folivorous insects. – *Acta Oecol.* 53: 19–32.
- King, D. A. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. – *Am. J. Bot.* 81: 948–957.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. – *Oecologia* 98: 419–428.
- Klawinski, P. D. et al. 2014. Coqui frog populations are negatively affected by canopy opening but not detritus deposition following an experimental hurricane in a tropical rainforest. – *For. Ecol. Manage.* 332: 118–123.
- Kobe, R. K. 1997. Carbohydrate allocation to storage as a basis of interest-specific variation in sapling survivorship and growth. – *Oikos* 80: 226–233.
- Letourneau, D. K. and Dyer, L. A. 1998. Experimental test in lowland tropical forest shows top-down effects through four trophic levels. – *Ecology* 79: 1678–1687.
- Levesque, K. R. et al. 2002. Temperature and food quality effects on growth, consumption and post-ingestive utilization efficiencies of the forest tent caterpillar *Malacosoma disstria* (Lepidoptera: Lasiocampidae). – *Bull. Entomol. Res.* 92: 127–136.
- Liang, Y. and Stehlik, I. 2009. Relationship between shade and herbivory in *Asarum canadense* (wild ginger). – *J. Undergraduate Life Sci.* 3.
- Lieth, H. et al. 1999. *Climate diagram world atlas*. – Backhuys Publishers B.V.
- Lieurance, D. and Cipollini, D. 2012. Damage levels from arthropod herbivores on *Lonicera maackii* suggest enemy release in its introduced range. – *Biol. Invas.* 14: 863–873.
- Lincoln, D. E. and Mooney, H. A. 1984. Herbivory on *Diplacus aurantiacus* shrubs in sun and shade. – *Oecologia* 64: 173–176.
- Lindroth, R. L. et al. 1997. Variation in temperature and dietary nitrogen affect performance of the gypsy moth (*Lymantria dispar* L.). – *Physiol. Entomol.* 22: 55–64.
- Löf, M. et al. 2005. The influence of different overstorey removal on planted spruce and several broadleaved tree species: survival, growth and pine weevil damage during three years. – *Ann. For. Sci.* 62: 237–244.
- Lopez-Toledo, L. et al. 2008. Soil and light effects on the sapling performance of the shade-tolerant species *Brosimum alicastrum* (Moraceae) in a Mexican tropical rain forest. – *J. Trop. Ecol.* 24: 629–637.
- Lowman, M. D. 1992. Leaf growth dynamics and herbivory in 5 species of Australian rain-forest canopy trees. – *J. Ecol.* 80: 433–447.
- Lusk, C. H. and Corcuera, L. 2011. Effects of light availability and growth rate on leaf lifespan of four temperate rainforest Proteaceae. – *Rev. Chil. Hist. Nat.* 84: 269–277.
- Lusk, C. H. and Piper, F. I. 2007. Seedling size influences relationships of shade tolerance with carbohydrate-storage patterns in a temperate rainforest. – *Funct. Ecol.* 21: 78–86.
- Lusk, C. H. and Reich, P. B. 2000. Relationships of leaf dark respiration with light environment and tissue nitrogen content in juveniles of 11 cold-temperate tree species. – *Oecologia* 123: 318–329.
- Lusk, C. H. et al. 2011. Latitude, solar elevation angles and gap-regenerating rain forest pioneers. – *J. Ecol.* 99: 491–502.
- MacArthur, R. H. 1969. Patterns of communities in the tropics. – *Biol. J. Linn. Soc.* 1: 19–30.
- McGeoch, M. A. and Gaston, K. J. 2000. Edge effects on the prevalence and mortality factors of *Phytomyza ilicis* (Diptera, Agromyzidae) in a suburban woodland. – *Ecol. Lett.* 3: 23–29.
- Moles, A. T. et al. 2011. Assessing the evidence for latitudinal gradients in plant defence and herbivory. – *Funct. Ecol.* 25: 380–388.
- Muth, N. Z. et al. 2008. Increased per capita herbivory in the shade: necessity, feedback or luxury consumption. – *Ecoscience* 15: 182–188.
- Myers, J. A. and Kitajima, K. 2007. Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. – *J. Ecol.* 95: 383–395.
- Naidu, S. L. and DeLucia, E. H. 1998. Physiological and morphological acclimation of shade-grown tree seedlings to late-season canopy gap formation. – *Plant Ecol.* 138: 27–40.
- Niesenbaum, R. A. 1992. The effects of light environment on herbivory and growth in the dioecious shrub *Lindera benzoin* (Lauraceae). – *Am. Midl. Nat.* 128: 270–275.
- Niesenbaum, R. A. and Kluger, E. C. 2006. When studying the effects of light on herbivory, should one consider temperature? The case of *Epimecis hortaria* F. (Lepidoptera: Geometridae) feeding on *Lindera benzoin* L. (Lauraceae). – *Environ. Entomol.* 35: 600–606.
- Niesenbaum, R. A. et al. 2006. Light, wind, and touch influence leaf chemistry and rates of herbivory in *Apocynum cannabinum* (Apocynaceae). – *Int. J. Plant Sci.* 167: 969–978.
- Norghauer, J. M. and Newbery, D. M. 2013. Herbivores equalize the seedling height growth of three dominant tree species in an African tropical rain forest. – *For. Ecol. Manage.* 310: 555–566.
- Norghauer, J. M. et al. 2008. Canopy cover mediates interactions between a specialist caterpillar and seedlings of a neotropical tree. – *J. Ecol.* 96: 103–113.
- Osier, T. L. and Jennings, S. M. 2007. Variability in host-plant quality for the larvae of a polyphagous insect folivore in midseason: the impact of light on three deciduous sapling species. – *Entomol. Exp. Appl.* 123: 159–166.

- Paritsis, J. and Veblen, T. T. 2010. Temperature and foliage quality affect performance of the outbreak defoliator *Ormiscodes amphimone* (F.) (Lepidoptera: Saturniidae) in northwestern Patagonia, Argentina. – *Rev. Chil. Hist. Nat.* 83: 593–603.
- Pearcy, R. W. 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. – *Funct. Ecol.* 1: 169–178.
- Pearson, T. R. H. et al. 2003a. Interactions of gap size and herbivory on establishment, growth and survival of three species of neotropical pioneer trees. – *J. Ecol.* 91: 785–796.
- Pearson, T. R. H. et al. 2003b. Regeneration niche partitioning in neotropical pioneers: effects of gap size, seasonal drought and herbivory on growth and survival. – *Oecologia* 137: 456–465.
- Piper, F. I. 2015. Patterns of carbon storage in relation to shade tolerance in southern South American species. – *Am. J. Bot.* 104: 654–662.
- Piper, F. I. et al. 2009. Carbohydrate storage, survival and growth of two evergreen *Nothofagus* species in two contrasting light environments. – *Ecol. Res.* 24: 1233–1241.
- Piper, F. I. et al. 2017. Carbon allocation to growth and storage in two evergreen species of contrasting successional status. – *Am. J. Bot.* 104: 1–9.
- Poorter, L. and Kitajima, K. 2007. Carbohydrate storage and light requirements of tropical moist and dry forest tree species. – *Ecology* 88: 1000–1011.
- Poorter, L. et al. 2010. Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. – *Ecology* 91: 2613–2627.
- Prather, C. 2014. Divergent responses of leaf herbivory to simulated hurricane effects in a rainforest understory. – *For. Ecol. Manage.* 332: 87–92.
- Richards, L. A. and Coley, P. D. 2007. Seasonal and habitat differences affect the impact of food and predation on herbivores: a comparison between gaps and understory of a tropical forest. – *Oikos* 116: 31–40.
- Richards, L. A. and Coley, P. D. 2008. Combined effects of host plant quality and predation on a tropical Lepidopteran: a comparison between treefall gaps and the understory in Panama. – *Biotropica* 40: 736–741.
- Ricklefs, R. E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. – *Am. Nat.* 111: 376–381.
- Rosenthal, J. P. and Kotanen, P. M. 1994. Terrestrial plant tolerance to herbivory. – *Trends Ecol. Evol.* 9: 145–148.
- Rosenthal, J. P. and Welter, S. C. 1995. Tolerance to herbivory by a stem-boring caterpillar in architecturally distinct maize and wild relatives. – *Oecologia* 102: 146–155.
- Salgado-Luarte, C. and Gianoli, E. 2010. Herbivory on temperate rainforest seedlings in sun and shade: resistance, tolerance and habitat distribution. – *PLoS One* 5: e11460.
- Salgado-Luarte, C. and Gianoli, E. 2012. Herbivores modify selection on plant functional traits in a temperate rainforest understory. – *Am. Nat.* 180: E42–E53.
- Schultz, T. D. 1998. The utilization of patchy thermal microhabitats by the ectothermic insect predator, *Cicindela sexguttata*. – *Ecol. Entomol.* 23: 444–450.
- Scriber, J. M. and Slansky, F. 1981. The nutritional ecology of immature insects. – *Annu. Rev. Entomol.* 26: 183–211.
- Shure, D. J. and Wilson, L. A. 1993. Patch-size effects on plant phenolics in successional openings of the southern Appalachians. – *Ecology* 74: 55–67.
- Sinimbu, G. et al. 2012. Do the antiherbivore traits of expanding leaves in the Neotropical tree *Inga paraensis* (Fabaceae) vary with light availability? – *Oecologia* 170: 669–676.
- Stoepler, T. M. and Lill, J. T. 2013. Direct and indirect effects of light environment generate ecological tradeoffs in herbivore performance and parasitism. – *Ecology* 94: 2299–2310.
- Stoepler, T. M. and Rehill, B. 2012. Forest habitat, not leaf phenotype, predicts late-season folivory of *Quercus alba* saplings. – *Funct. Ecol.* 26: 1205–1213.
- Takafumi, H. et al. 2010. Herbivory in canopy gaps created by a typhoon varies by understory plant leaf phenology. – *Ecol. Entomol.* 35: 576–585.
- Tauber, C. A. et al. 1987. Thermal requirements for development in *Chrysopa oculata*: a geographically stable trait. – *Ecology* 68: 1479–1487.
- Tiffin, P. and Rausher, M. D. 1999. Genetic constraints and selection acting on tolerance to herbivory in the common morning glory *Ipomoea purpurea*. – *Am. Nat.* 154: 700–716.
- Vincent, G. 2006. Leaf life span plasticity in tropical seedlings grown under contrasting light regimes. – *Ann. Bot.* 97: 245–255.
- Walters, M. B. and Reich, P. B. 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? – *New Phytol.* 143: 143–154.
- Whitmore, T. C. and Brown, N. D. 1996. Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. – *Phil. Trans. R. Soc. B* 351: 1195–1203.
- Zhang, S. et al. 2016. Latitudinal variation in herbivory: hemispheric asymmetries and the role of climatic drivers. – *J. Ecol.* 104: 1089–1095.
- Zhang, Y. et al. 2011. Does insect folivory vary with latitude among temperate deciduous forests? – *Ecol. Res.* 26: 377–383.

Supplementary material (available online as Appendix oik-04686 at <www.oikosjournal.org/appendix/oik-04686>). Appendix 1–2.