Canadian Science Publishing

NOTE

An experimental approach for crown to whole-canopy defoliation in forests

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Abstract: Canopy defoliation is an important source of disturbance in forest ecosystems that has rarely been represented in large-scale manipulation experiments. Scalable crown to canopy level experimental defoliation is needed to disentangle the effects of variable intensity, timing, and frequency on forest structure, function, and mortality. We present a novel pressure-washing-based defoliation method that can be implemented at the canopy-scale, throughout the canopy volume, targeted to individual leaves or trees, and completed within a timeframe of hours or days. Pressure washing proved successful at producing consistent leaf-level and whole-canopy defoliation, with 10%–20% reduction in leaf area index and consistent leaf surface area removal across branches and species. This method allows for stand-scale experimentation on defoliation disturbance in forested ecosystems and has the potential for broad application. Studies utilizing this standardized method could promote mechanistic understanding of defoliation effects on ecosystem structure and function and development of synthetic understanding across forest types, ecoregions, and defoliation sources.

Key words: defoliation, experiment, herbivory, canopy, disturbance.

Résumé : La défoliation du couvert forestier est une source importante de perturbation dans les écosystèmes forestiers qui a rarement été étudiée dans des expériences de manipulation à grande échelle. Une défoliation expérimentale transposable de l'échelle de la cime à celle du couvert forestier est nécessaire pour distinguer les effets de la variation de l'intensité, du moment et de la fréquence sur la structure, la fonction et la mortalité de la forêt. Nous présentons une nouvelle méthode de défoliation fondée sur le lavage à la pression qui peut être : appliquée à l'échelle du couvert forestier, à tout le volume du couvert forestier, appliquée à des arbres ou des feuilles individuellement et réalisée à l'intérieur d'une période de quelques heures à quelques jours. Le lavage à la pression a réussi à produire une défoliation constante à l'échelle des feuilles et de l'ensemble du couvert forestier avec une réduction de 10–20 % de l'indice de surface foliaire et l'élimination d'une surface foliaire constante parmi les branches et les espèces. Cette méthode permet d'expérimenter à l'échelle du peuplement avec les perturbations causées par une défoliation dans les écosystèmes forestiers et pourrait avoir un vaste champ d'application. Des études utilisant cette méthode standardisée pourraient faciliter la compréhension mécaniste des effets de la défoliation sur les fonctions et la structure des écosystèmes ainsi que la compréhension synthétique des types forestiers, des écorégions et des sources de défoliation. [Traduit par la Rédaction]

Mots-clés : défoliation, expérimentation, broutage, couvert forestier, perturbation.

1. Introduction

Large-scale experimental manipulations have been essential to advancing knowledge about ecosystem processes (e.g., Ainsworth and Long 2005; Templer et al. 2017). For example, experiments emulating variable disturbance severity, timing, frequency, and extent have produced substantial understanding of the impacts of disturbance on ecosystem structure and function (e.g., Ellison et al. 2010; Gough et al. 2013). In some cases, experimental manipulations utilize or closely mimic actual disturbance mechanisms, such as controlled burning to emulate wildfire disturbance (e.g., Peterson and Reich 2001) or water spraying in sub-zero conditions to emulate ice storm damage (Rustad and Campbell 2012). Other experiments have used more artificial techniques to disturb forest canopies, such as stem girdling to emulate phloem disruption (Gough et al. 2013), or mechanical winching to simulate wind throw (Plotkin et al. 2013). In global change experiments, disturbances are often emulated through individual organism to ecosystem-scale manipulations of environmental stressors, such as rain-out shelters in drought experiments (Gherardi and Sala 2013) or soil heating systems (Templer et al. 2017). Together, the many large-scale disturbance experiments implemented by ecologists have contributed to cross-disturbance synthesis work (Hicke et al. 2012) and aided in modeling the effects of disturbance on ecosystem structure and function (Dietze and Matthes 2014).

Among the numerous forms of disturbance mimicked experimentally, canopy defoliation stands out as an important source of disturbance in forest ecosystems that has rarely been represented in large-scale manipulation experiments despite its massive global impact and increasing extent (Anderegg et al. 2015;

Received 18 December 2020. Accepted 17 April 2021.

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Can. J. For. Res. **52:** 286–292 (2022) dx.doi.org/10.1139/cjfr-2020-0527

Fei et al. 2019). Defoliation can occur as a result of herbivory, pathogens, or through mechanical means (e.g., hailstorms or hurricanes; Dobbs and McMinn 1973; Shiels et al. 2014). Most extensive and severe defoliation events are related to insect pests, and patterns of defoliation timing and intensity vary, with cyclical, outbreak, and background herbivory all common in nature (Kautz et al. 2017). In deciduous forests with short leaf lifespans, canopy defoliation often results in only partial or temporary disturbance and sub-mortality effect on trees, whereas in evergreen species (needle-leaf or broad-leaf) defoliation is more likely to result in mortality (Foster 2017). Defoliation events often occur as multi-year outbreaks with high mortality rates resulting after consecutive growing seasons, prompting a cascade of effects on ecosystem structure and function (Morin and Liebhold 2016; Chen et al. 2017). Defoliation can also interact with other disturbances (such as drought or wind), with the potential to have amplifying effects on mortality and ecosystem structure and function (Anderegg et al. 2015; Buma 2015).

In the absence of a scalable experimental approach, research on the structural and functional effects of defoliation at the ecosystem scale in forests has been largely associated with opportunistic and retrospective field studies (e.g., Stephens et al. 1972; Lovett et al. 2002) or modeling experiments (Medvigy et al. 2012). Experimental defoliation has largely been limited to assessment of effects on individual plants and crowns using clipping, hole-punching, and leaf mutilation — with studies primarily conducted in controlled environments such as greenhouses and growth chambers (Hjalten et al. 1993; Krause and Raffa 1996; Tong et al. 2003; Wu et al. 2020). While the combination of the above types of studies have contributed greatly to our understanding of the effects of defoliation and the mechanistic basis of leaf and plant responses, there is a need to represent herbivory and other defoliation experimentally and at the scale that ecosystem and community processes occur. Large-scale experimentally induced defoliation is critical to unraveling several knowledge gaps related to defoliation effects on mortality outcomes and alteration of ecosystem structure and function. For example, ecosystem-scale experimental defoliation is necessary to isolate the effects of variable defoliation sources, intensity, timing, and frequency and separate these disturbance characteristics from co-varying factors such as climate, soils, or forest composition (Atkins et al. 2020). In addition, as the frequency, distribution, and severity of other forms of disturbance changes, experimental work focused on disentangling the interaction of defoliation with other disturbance agents will be essential to predicting and modeling forest ecosystem response and functioning (Anderegg et al. 2015; Buma 2015). Experimental manipulations could also greatly enhance our ability to evaluate and model the potential future impact of novel defoliators and combinations of disturbances on ecosystem processes such as carbon sequestration and nutrient cycling (Anderegg et al. 2015; Buma 2015). To date, there has been no widely accepted method to produce stand- or ecosystem-scale defoliation in vegetation canopies. Here, we present a new method for experimental canopy defoliation in forests and other vegetated ecosystems, detail results of a pilot study aimed at developing and testing the method, and discuss its broad applicability and utility.

2. Materials and implementation

Canopy defoliation events may be spatially and temporally diffuse disturbances that affect all layers of the canopy concurrently, but, alternatively, defoliation may occur dynamically in space and time (e.g., affecting specific species; Campbell and Sloan 1977). Disturbances unfold over a range of time scales, from a matter of minutes (e.g., in a hail storm; Dobbs and McMinn 1973) to weeks or months (e.g., in an insect herbivore outbreak; Schowalter et al. 1986). Thus, the goal of this method development was to design a flexible and scalable experimental approach that could be implemented throughout the canopy volume, be targeted to individual leaves, trees, or whole canopies, and secondarily, be completed within a timeframe of hours to days depending on the intensity and spatial extent of manipulation.

Our experimental method uses a high-pressure water stream applied at close proximity to the leaf or twig to defoliate tree branches and crowns. Initial tests indicated that a medium to heavy duty (2000–3000 PSI) consumer-grade pressure washer produced enough force to perforate leaves or remove them completely from the twig, but produced very limited damage to twigs, bark, and buds (e.g., supplementary Fig. S5[1]). However, close proximity of the pressure washer nozzle to the leaf (<1 m) was needed to produce this effect (and was also necessary to allow for discrimination and targeting of individual leaves or branches). Therefore, to experimentally emulate a whole-, and particularly upper, canopy defoliation event using a pressure washer, it was necessary to have a canopy access system that could be positioned within 1 m of the targeted canopy area.

Many different canopy access strategies have been utilized in forest ecology research, including tree climbing, rope networks, fixed or semi-permanent towers, and maneuverable lift vehicles (Barker and Pinard 2001). We utilized a 20-m-high maneuverable, off-road, lift platform vehicle (Fig. 1*d*; supplementary Fig. S3[1]), which provided interior forest access via small woods roads or skid trails, upper canopy access (to the 22-m-tall canopy), a stable aerial platform (Fig. 1*e*), and platform maneuverability within the canopy once aloft (supplementary Fig. S4[1]). These types of lift vehicles are not specialized research equipment, require relatively minimal training to operate, and are commonly used in construction and utility fields making them potentially available on or near campuses and other locations where research occurs. To facilitate defoliation from the aerial platform, we utilized a 33-m-long high-pressure hose attached to the pressure washer on the ground (Fig. 1*c*), a long (1.5 m) wand nozzle (Fig. 1*f*), and we utilized a large water tank (~1800 L) to provide ample water for the pressure-washing-based defoliation (Fig. 1*b*); water was pumped from a nearby lake and transported to the study site in a standard medium-duty pickup truck.

We tested the canopy defoliation method during the height of the growing season (mid-July) in a maturing deciduous forest at the University of Michigan Biological Station (Gough et al. 2013) representative of mixed hardwood forests that occur across the northern temperate zone (canopy height 20–30 m, leaf area index (LAI) 3–4, with dominance by *Quercus*, *Acer*, and *Fagus* species; Table 1). Our goal was to demonstrate the feasibility of creating defoliation across a defined plot area and canopy volume; therefore, we delineated three 100 m^2 (10 m × 10 m square) experimental demonstration plots along a "two-track" forest access road with variable starting structure and composition (Table 1). Within each experimental plot, we worked for a defined amount of time (~5 h, with some variation due to weather conditions) to assess whether the method would produce equivalent defoliation levels per unit time invested across different plots. For this test, we attempted to produce similar levels of defoliation across the vertical profile and through horizontal space and did not discriminate by species; however, some small areas of the canopy were not accessible with the lift vehicle bucket and defoliation severity was thus not strictly equivalent across the canopy volume.

To evaluate the level of defoliation produced by the treatment to individual leaves and branches of the three canopy tree species that occurred on the plots (Table 1), we surveyed damage to leaves on treated branches (Table 1) collected from different levels above the ground within treated and compared treated branches to randomly selected branches from the same height levels in a paired adjacent control plot. We clipped branches selected systematically

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[1] Supplementary data are available with the article at https://doi.org/10.1139/cjfr-2020-0527.

Fig. 1. Canopy defoliation and monitoring system, including (*a*) ~1-m-diameter plastic pool with drainage holes used to collect leaf fragments, (*b*) 1893 L (500 US gallon) water tank, (*c*) medium-duty (2400 PSI) consumer-grade pressure washer, (*d*) 20-m-elevation maneuverable, off-road, lift platform vehicle, with (*e*) stable aerial platform, and (*f*) 33-m-long high-pressure hose with 1.5 m wand nozzle (photograph depicts co-author J. Atkins; all photographs by D. Tanzer and R. Fahey). [Colour online.]

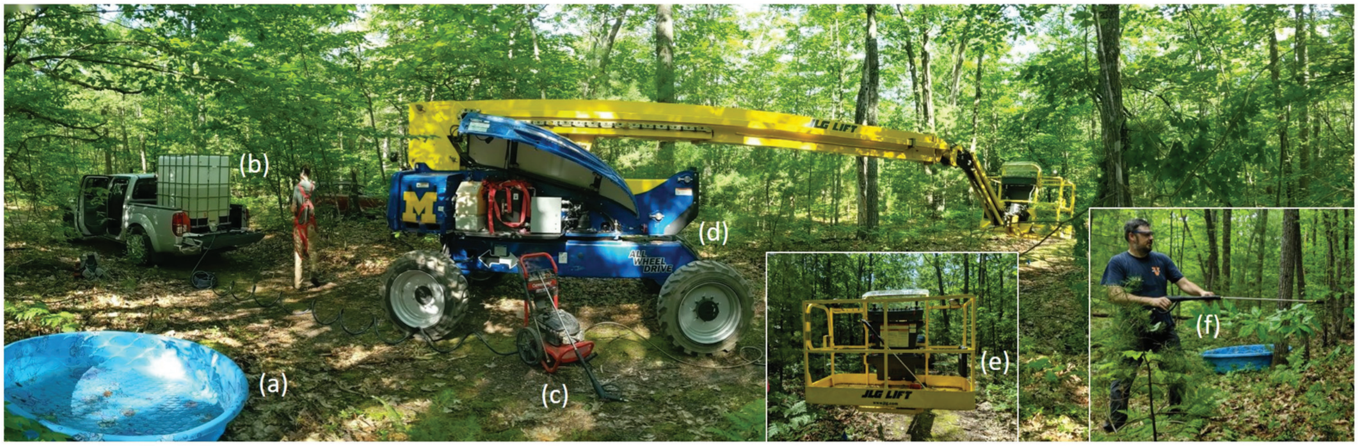


Table 1. Details on application of experimental defoliation across three 10 m × 10 m study plots.

Plot	0-10E	20-30W	30-40E
Time	4.5 h	5 h	5 h
Water used	660 L	560 L	470 L
Treatment "precipitation" input	6.6 mm	5.6 mm	4.7 mm
LAI change	–16.0%	–13.6%	–15.1%
Species composition (% of basal area)	QURU 75% ACRU 15% FAGR 10%	QURU 74% ACRU 14% FAGR 2%	QURU 61% ACRU 38% FAGR 1%
No. of canopy trees >10 cm	8	6	6

Note: LAI, leaf area index; QURU, *Quercus rubra*; ACRU, *Acer rubrum*; FAGR, *Fagus grandifolia*.

within three height intervals (0–5 m, 5–10 m, 10+ m) at random ground (i.e., XY) locations within the plot without regard to visual damage assessment but within areas affected by the defoliation (three for each of the three dominant species in each treated plot and a control plot — 12 branches per species total across the four plots). For each branch, we visually categorized the percent damage for each leaf and produced a count of leaves in each of six damage categories (0, >0–25, 25–50, 50–75, 75–<100, 100%; Fig. 2*b*). We then removed all of the leaves from these branches, and from these collections of leaves (treatment and control for each species), we randomly selected 30 leaves of each species (20 from treated, 10 from control – 90 total across the three species; Fig. 2*a*; supplementary Figs. S6-S8[1]) for image-based analysis of leaf area using ImageJ. For each species, we compared the mean leaf area of all leaves collected within treatment plots to that of leaves collected in Control plots using analysis of variance (ANOVA).

To assess the effects of the experimental treatment on whole-canopy structural metrics tied to ecosystem functioning (Fahey et al. 2019) and to compare to natural defoliation disturbances, we collected several types of pre- and post-treatment data at the plot level (all <1 week before or after treatment). We collected north-oriented, levelled, hemispherical canopy photographs under uniformly cloudy conditions at 1 m height in four locations in each plot (supplementary Figs. S1 and S2[1]) and used WinSCANOPY (Regent Instruments) to calculate leaf area index, gap fraction, and gap light index for zenith angles 0°–60° (LAI 4 ring) in the resulting images. During the treatment we also collected leaf litter using three 1-m-diameter plastic pools (Fig. 1*a*; supplementary Fig. S11[1]). Following treatment, leaf fragments were collected, dried, and weighed and a subset was scanned for leaf area (prior to drying). The dry weight and total surface area of the scanned subset was used to estimate leaf surface area removed by the treatment at the plot scale (supplementary Table S1[1]). We collected data on the fraction of photosynthetically active radiation (fPAR) transmitted through the canopy to 1 m height under full sun conditions between 10:00 am and 2:00 pm using a Decagon LP-80 Ceptometer (Meter Group Inc.) at 1 m intervals along five transects arrayed in parallel at 2 m spacing through the plot (supplementary Fig. S1[1]). Along the same transects, we collected vertical and horizontal canopy structural information using a Portable Canopy Lidar system and calculated canopy structural metrics using the FORESTR R package (Atkins et al. 2018). Canopy structural characteristics were compared between pre- and post-treatment conditions using one-way repeated measures ANOVA using SAS version 9.4 (SAS Inc.).

3. Results

The pressure-washing defoliation method proved successful at producing a consistent leaf-level and whole-canopy defoliation per unit time invested in the 10 m × 10 m test plots. Expansion to greater plot area may scale linearly (assuming canopy accessibility) based on the consistent results from the three test plots (Table 1). A defoliation level of ~15% LAI reduction was achieved in each plot over the course of the ~5 h period of application (Figs. 2*c*, 2*d*). Greater defoliation severity within a manipulated area could likely be achieved with additional time input (or with multiple concurrent operators), but whether the relationship between time and defoliation level would be linear at higher severity levels was not

Fig. 2. Images depicting different scales at which the effects of experimental defoliation were assessed, including (*a*) leaf-level surface area and removal compared between control and treated leaves, (*b*) branch-level analysis of consistency of leaf surface area removal, and (*c*) pre- and (*d*) post-treatment assessment of canopy-scale cover and light transmittance. All photographs by R.T. Fahey. [Colour online.]

tested in this pilot study. The most effective method for creating leaf damage phenomenologically similar to natural defoliation (i.e., partial removal of surface area from individual leaves rather than complete removal from the twig at the petiole; Fig. 2*a*) was a pulsing of the water stream from the pressure washer (see video in supplementary material[1]). This method also required less water input, which is reflected in the somewhat higher level of water used in the first experimental plot (0-10E) before the pulsing method was consistently employed (Table 1). Across all treatments, the level of water needed to produce the defoliation was less than initially expected, and a single water tank (fillable in matter of minutes using a standard water pump) was more than sufficient to produce the desired defoliation levels (and potentially up to 3× this level assuming a linear relationship).

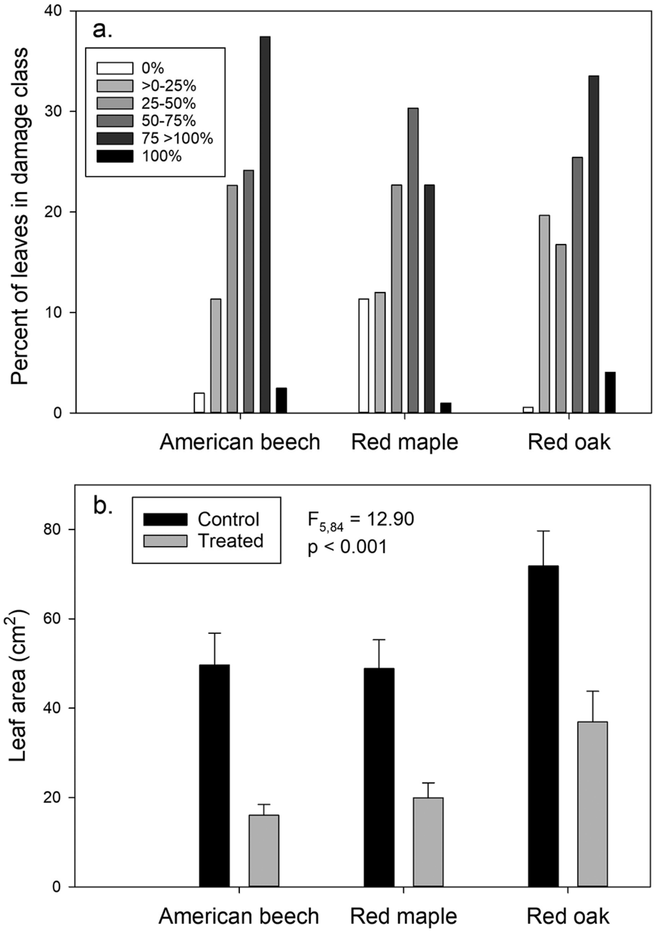
The branch-level reduction in leaf surface area produced by the treatment was generally consistent across branches positioned throughout the canopy and also across the three primary tree species represented in the plots (Fig. 3*a*). The distribution of leaf surface area removal within treated branches had an approximately normal distribution, but with a majority of leaves exhibiting >75% damage for both American beech (*Fagus grandifolia* Ehrh.) and red oak (*Quercus rubra* L.) (Fig. 3*a*). For each of the species, very few leaves (<5%) were removed at the petiole (i.e., 100% damage). Mean leaf area for treated branches was reduced by >50% for both red maple (*Acer rubrum* L.) and American beech, and by nearly 50% for red oak, relative to control leaves from adjacent plots (Fig. 3*b*). These numbers are for treated branches only and, thus, are not representative of the overall canopy leaf area removal, which was characterized by hemispherical photography.

The canopy-level defoliation results showed a significant increase in gap light index and decrease in LAI, which declined between 10% and 20% in each plot (Fig. 4). LAI was reduced by approximately 0.5 units in each plot, on average from 3.6 to 3.1, representing the removal of a half of a full leaf layer from the canopy volume (Fig. 4; validated by litter collection data — supplementary Table S1[1]). These defoliation levels are greater than the baseline interannual variability in LAI in the system (Gough et al. 2013) and are consistent with low–moderate severity canopy defoliations resulting from insect herbivory and physical defoliation by hail or ice storms (Davidson et al. 1999; Fahey et al. 2020). The proportion of above-canopy photosynthetically active radiation transmitted through the canopy (fPAR) increased by an average of 11% across the three plots, but levels were highly variable across the plots and not statistically significant different from pre- to post-treatment ($F_{[1,14]} = 0.54$, $p = 0.48$). Canopy interior vertical structure was also affected by the treatment with mean leaf height increasing (likely due to difficulty of reaching very upper canopy foliage, which could be avoided in future implementations with more explicit targeting of the top of the canopy), variance in mean leaf height decreasing, and rugosity (canopy complexity) increasing significantly following the treatment (Fig. 5).

4. Discussion

The novel, scalable canopy-level defoliation method presented here can increase the efficiency and spatial scale of defoliation experiments and allow researchers to plan defoliation or even react to specific environmental conditions (e.g., natural drought) to quickly implement defoliation, which could be highly valuable

Fig. 3. Analysis of branch- and leaf-level defoliation illustrating (*a*) frequency distribution of leaf surface area removal across treated branches of three primary species and (*b*) comparison of leaf surface area between leaves from treated branches and untreated control branches. Results of ANOVA comparing treated and control are indicated.



in promoting new understanding of the effects of defoliation on forest ecosystem structure and function, especially by allowing a closer approximation of natural disturbance and disturbance interactions. For example, the application of this whole-canopy defoliation method could allow for experimental comparison of the functional outcomes of rapid herbivory-based defoliation and slower-acting defoliation from phloem girdling (Hicke et al. 2012; Gough et al. 2013), two primary types of pest-associated disturbance. The reliance of prior experimental studies on individual leaf, twig, or branch cutting or hole-punching and focus on smaller individuals has limited their scope and realism for understanding the effects of tree to canopy-scale defoliation (Shiels et al. 2014; Wu et al. 2020). The ability to move from individual branch or crown to canopy, population, or ecosystem-scale manipulations could represent a major step forward in understanding defoliation effects on processes such as competition, regeneration, and biogeochemical cycling that play out beyond the individual tree level (Hicke et al. 2012; Chen et al. 2017; Fei et al. 2019). This expansion of spatial scale from individual to canopy is akin to the shift from chamber to free-air CO_2 enrichment that massively increased understanding of forest responses to increasing atmospheric CO_2 levels (Ainsworth and Long 2005). As with other experimental techniques such as rain-out shelters used in the Drought-Net network (Gherardi and Sala 2013), a standardized method for producing canopy-level defoliation could eventually promote the development of a multi-site network of manipulative experiments and lead to a synthetic understanding of defoliation effects across forest types and ecoregions that cannot be gained from opportunistic observational studies.

The method introduced here has several additional strengths including modest time and effort investment, the ability to modulate spatial and temporal aspects of defoliation, as well as the potential to implement fine-scale and targeted variation in defoliation intensity at the whole-canopy scale. The effort applied here of <5 h with only two personnel yielded canopy-scale defoliation levels comparable to those observed following natural defoliation, which would likely require weeks of work from a large field crew using manual clipping methods (Shiels et al. 2014; Wu et al. 2020). In addition to savings in resources, this also allows for much greater flexibility in application and the potential to test more specific ranges of defoliation patterns both temporally and spatially. The time investment required for methods such as leaf clipping has historically made it infeasible to match the temporal scale at which herbivory impacts an entire forest canopy. The potential to explicitly match the timing and duration of a natural defoliation event (based on prior knowledge of specific agents in the ecosystem in question) at the stand or ecosystem scale could be highly valuable to assessing the effects of these disturbances on ecosystem processes. The timing and duration of defoliation could also be manipulated to allow investigation of the effects of changing canopy or herbivory phenology on defoliation outcomes. In addition, specific fine-scale spatial targeting of defoliation impacts can facilitate experimental manipulation of defoliation distribution vertically and horizontally within a canopy as well as among species and individuals.

Although this method could have broad applicability and substantial impact, there are several limitations and unknowns that should be noted. Based on our initial experience, the power-washing technique may have limited utility in conifer-dominated forests, may be difficult to apply at a multi-tree, whole-canopy scale in forests with very large individual tree crowns, and the access strategy may be limited in difficult terrain and remote locations and restricted to lower canopy strata in very tall forests, although other access methods are possible, including canopy cranes or fixed towers (Barker and Pinard 2001). Like numerous other commonly applied and influential disturbance manipulations (Rustad and Campbell 2012; Gough et al. 2013), the approach presented here does not entirely mimic the biological implications or consequences of herbivore defoliation. For example, herbivory by insects results in substantial chemical defense responses by trees stimulated by pheromone signaling, and insect herbivory is likely to be nonrandom and related to variation in the chemical and nutrient status of foliage (Schowalter et al. 1986). The effects of experimental defoliation and insect herbivory on nutrient cycling may not be equivalent because of the difference between inputs of frass versus physically deconstructed leaf fragments (Lovett et al. 2002). The input of water, although in relatively minor amounts (less than 1% of the mean annual precipitation of 817 mm at the site; Table 1), could also affect ecosystem processes and any experimental framework would require equivalent amounts of water be applied to controls and studies focused on drought interactions may require tarps to preclude water inputs into the system. Finally, diminishing returns in the time–defoliation relationship may somewhat restrict the method to low or moderate levels of defoliation, but this relationship likely differs among forest types and with canopy access.

Fig. 4. Results of analysis of hemispherical canopy images comparing pre- and post-treatment conditions for (*a*) gap fraction as a percent of total area, (*b*) gap light index as estimated percent transmitted above-canopy radiation at the 1 m photograph height, and (*c*) leaf area index. Results of ANOVA comparing pre- and post-treatment conditions are indicated.

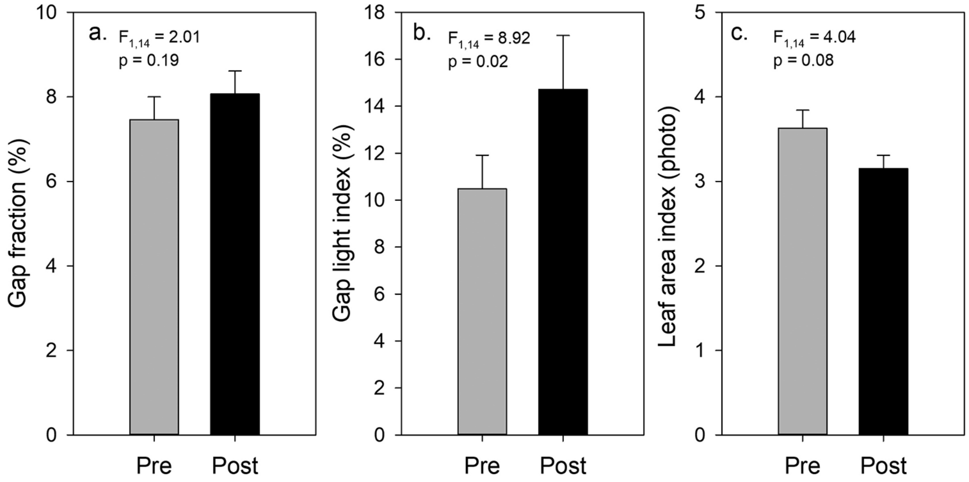
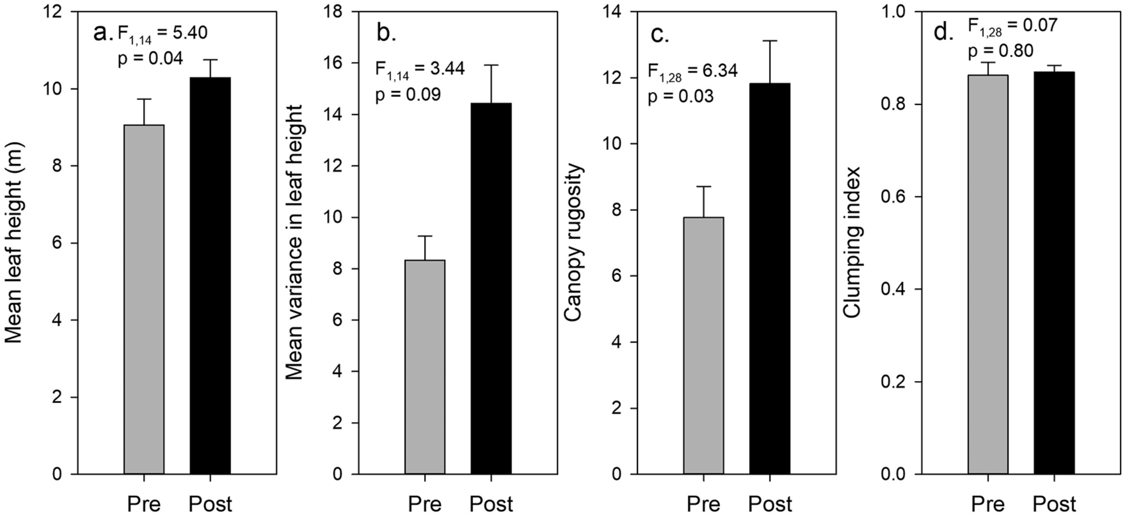


Fig. 5. Results from terrestrial LiDAR analysis of canopy structure metrics (Atkins et al. 2018) comparing pre- and post-treatment conditions for (*a*) mean vegetation height, (*b*) mean variance in vegetation height across 1-m-wide columns, (*c*) canopy rugosity as the standard deviation across 1-m-wide columns in the standard deviation of vertical vegetation height within columns, and (*d*) clumping index — a measure of vegetation grouping relative to a random distribution. Results of ANOVA comparing pre- and post-treatment conditions are indicated.



Contributors' statement

RF, JA, CG, and BH conceived the ideas and designed methodology; RF, JA, BH, CG, and DT collected the data; DT, BA, JA, and RF analyzed the data; RF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Funding

Funding for this work was provided by the UConn Research Excellence Program. Funding for the AmeriFlux core site (US-UMB) within which the test study was conducted was provided by the U.S. Department of Energy's Office of Science.

Data availability

Data will be archived in the University of Michigan Biological Station Mfield Data Repository: https://mfield.umich.edu/.

Acknowledgements

This research is a product of the University of Michigan Biological Station, and the efforts of Scott Haley, Richard Spray, Jason Tallant, and Adam Schubel are especially appreciated.

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