

RESPONSE OF PLANT PATHOGENS AND HERBIVORES TO A WARMING EXPERIMENT

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Abstract. Pathogens and herbivores can severely reduce host fitness, potentially leading to altered succession rates and changes in plant community composition. Thus, to predict vegetation dynamics under climate change, it is necessary to understand how plant pathogens and herbivores will respond. Pathogens and herbivores are predicted to increase under climate warming because the amount of time available for growth and reproduction will increase. To test this prediction, we used a warming experiment in which heaters were suspended over a natural montane meadow for 12 years. In the summer of 2002, we quantified damage by all the observable (aboveground) pathogens and herbivores on six of the most common plant species (*Artemisia tridentata*, *Helianthella quinquenervis*, *Erigeron speciosus*, *Potentilla gracilis*, *Potentilla hippiana*, and *Lathyrus leucanthus*). We found that plants in the earlier melting plots generally had the most damage and were attacked by a larger number of species, which is consistent with predictions. However, although the overall trend was an increase in damage with warmer temperatures and earlier snowmelt, some pathogens and herbivores performed better in cooler or later melting plots. The idiosyncratic response of each species to environmental conditions suggests that there are likely to be changes in community composition as the planet warms.

Key words: *Artemisia tridentata*; CO_2 ; *Erigeron speciosus*; climate change; global warming; *Helianthella quinquenervis*; herbivory; *Lathyrus leucanthus*; plant pathogens; sagebrush; *Potentilla gracilis*; *Potentilla hippiana*.

INTRODUCTION

There is increasing evidence for global climate change as a result of anthropogenic production of CO_2 and other greenhouse gases (IPCC 2001). One of the major ecological consequences of climate change is that vegetation over large areas is predicted to change dramatically because plants are sensitive to changes in temperature and precipitation (Bonan et al. 1995, Foley et al. 2003, Root et al. 2003). Not only does climate influence vegetation, but the plants in turn influence climate through their use and storage of carbon, water relations, and albedo (Nobel 1991, Bonan et al. 1992, Harte and Shaw 1995, Loik and Harte 1997). The specific effects of vegetation on climate depend on the characteristics of the dominant vegetation types (Bonan et al. 1995, Foley et al. 2003). It is therefore important for predictive purposes to understand how climate change will influence plant species composition across broad regions.

Climate change may also influence the distribution and abundance of plants indirectly through modifying their pathogens and herbivores (Lonsdale and Gibbs 1996, Coakley et al. 1999, Ayres and Lombardero

2000). These organisms can be important in structuring plant populations and communities because they often reduce the survival and reproduction of their hosts. For example, a pathogen that utterly changed a community is the chestnut blight that swept through forests in Eastern North America in the first half of the 20th century, reducing the basal area of chestnut from 31% to 0.1% in the Appalachian Mountains (Day and Monk 1974). Herbivores are also well known for reducing host fitness, and for affecting plant community composition (Marquis 1992).

The reduction of host fitness caused by pathogens and herbivores is often exacerbated when the host is under physiological stress (Colhoun 1973, Louda 1987, Collinge and Louda 1988, Jarosz and Burdon 1988). Drought stress in plants, for example, is expected to increase with warming (IPCC 1998, Barber et al. 2000). Stressed plants might have higher attack rates, either due to physical damage allowing access (Hanson and Weltzin 2000), or due to physiological diversion of resources from defense to maintenance (Larsson 1989).

The principle prediction for herbivores under warming conditions is that they will increase because warmer temperatures tend to accelerate insect development and reproduction (Ayres 1993, Malmström and Raffa 2000). Less is known about how global warming might influence plant pathogens (Coakley et al. 1999, Ayres and Lombardero 2000) or how pathogens and herbi-

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vores may collectively interact with climate change to influence plant distributions (Harvell et al. 2002).

We used an ongoing experimental manipulation in the Rocky Mountains of Colorado, USA, to assess pathogen and herbivore damage on six plant species growing in heated and unheated experimental plots. The heaters have been on for 12 years, so there has been ample time for the herbivore and pathogen populations to have adjusted to the temperature and temperature-induced changes in the hosts. An advantage of studying this long-term manipulation experiment is that numerous measurements have been made on the same plots of meteorological (Harte et al. 1995), biogeochemical (Torn and Harte 1995, Shaw and Harte 2001, Saleska et al. 2002), and plant characteristics (Harte and Shaw 1995, Loik and Harte 1996, 1997, Price and Waser 1998, De Valpine and Harte 2001).

Specifically, we asked the following questions: (1) Did the heating treatment influence the amount of overall damage (i.e., that caused by pathogens and herbivores combined)? (2) Did the heating treatment influence the number of species that attacked the plants? (3) Did pathogens and herbivores respond to heating in the same ways? (4) How did the heating treatment affect individual species of pathogens and herbivores? (5) How did the heating treatment affect tritrophic interactions between plants, herbivores and the parasitoids and predators of the herbivores?

MATERIALS AND METHODS

Warming experiment design

In 1990, a “meadow warming” experiment was initiated in a montane meadow near the Rocky Mountain Biological laboratory in Colorado, USA (38°53' N, 107°02' W) at 2920 m (see Plate 1). The experimental design and other results have been detailed elsewhere (Harte and Shaw 1995, Harte et al. 1995, 1996, Loik and Harte 1996, 1997); therefore, the experiment will only be briefly described here. To investigate ecological responses to an increase in surface warming comparable to that expected under two-times CO₂, radiant infrared heaters (Kalglo, Lehigh, Pennsylvania, USA) were suspended over five 3 × 10 m plots. The five heated plots were systematically alternated with five control plots, which were the same size but without heaters. The heaters have been on continuously since the experiment began in 1990. The heaters warm the soil to a 12 cm depth by 1.5°C and dry it 15% (that is, 40% gravimetric in controls would be matched by 34% gravimetric in the heated plots; 34 is 15% less than 40), averaged over the growing season.

Plant species monitored for pathogens and herbivores

We examined damage (percentage of tissue removed) on all the plant species present in the plots for which there were sufficient replication of individuals (~10/



PLATE 1. Meadow warming experiment at the Rocky Mountain Biological Laboratory in winter. The main influence of the heaters was to cause earlier snow melt. Photo credit: S. Saleska.

plot) to compare within-plot variation with among-plot variation. The plant species we examined were: *Potentilla gracilis* Douglas (Rosaceae), *Potentilla hippiana* Lehmann (Rosaceae), *Helianthella quinquenervis* (Hooker) Gray (Asteraceae), *Artemisia tridentata* Nutt. (Asteraceae), *Erigeron speciosus* (Lindley) de Candolle (Asteraceae), and *Lathyrus leucanthus* Greene (Fabaceae). Measurements of damage on each plant species were taken over a 4-d period in late May 2002 (*Artemisia* and *Lathyrus*) or over a 5-d period in early July 2002 (the remainder of the taxa).

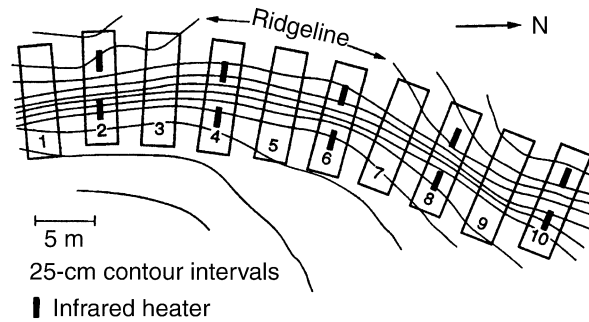
Sampling, parasite identification, and measurements

Sampling methods depended on the number and size of the individual host species. When the host species was small and numerous (e.g., *Lathyrus*), we measured a random sample of plants from each plot by centering a single 1-m² quadrat that was divided into 16 squares (0.25 m² on a side) under the middle heater. We then measured (when present) the stem closest to the center of each of the 16 squares. When the host species was large and thus not represented by many individuals in each plot (e.g., *Artemisia*, *Erigeron*, *Helianthella*, *Potentilla* spp.), we measured all the individuals in each plot that were within the one meter strip centered directly under the heaters or in the same relative location in the control plots. We recorded all the observable damage (percentage of area of tissue removed) on all aboveground parts (*Lathyrus*), or on a set of three leaves, each taken from the top, middle, and basal part of the plant (*Erigeron*, *Helianthella*, *Potentilla* spp.), or counted the number of stems showing particular kinds of damage (*Artemisia*).

We determined what caused the different kinds of damage (pathogen, herbivore, environmental such as frost, or unknown) through careful field and microscopic observation. We collected specimens of each

Treatment	C	H	C	H	C	H	C	H	C	H
Melt date	109	95	109	103	104	95	99	85	94	82

FIG. 1. Experimental design, showing the position and aspect of the plots, as well as the treatment (H, heated; C, control) and the day of year (day 1 = January 1) of snowmelt for the year (2002) in which the measurements were made.



kind of damage, and most were also photographed under $4\times$ magnification in the field. All the pathogens we identified were fungal. For a particular kind of damage to be declared as being caused by a fungal pathogen, definitive characteristics such as spores, hyphae, or asci had to be observed on the sample. When it was possible to determine the fungal species based on morphology, we did so (many pathogens require culturing and sequencing for species determination). With the insects, we were often able to directly observe them causing particular kinds of damage. One of our hosts, *A. tridentata*, was attacked by large numbers of aphids. The aphids attracted ants, which tended them, and parasitoids, which parasitized them. Furthermore, the ants and aphids attracted spiders. We quantified these tritrophic interactions along with the pathogen measurements by counting the number of ants, parasitized aphids, and spiders on the plants.

We estimated damage as a percentage of leaf area removed for all of the host species except *Artemisia tridentata*. *A. tridentata* is a shrub and thus has many more stems and leaves than the forbs. For this species, we counted the number of stems with damaged leaves per individual. We did not count the number of undamaged stems, but instead measured shrub diameter under the assumption that total number of stems would be strongly positively correlated with size. For this reason, all analyses with *A. tridentata* included the covariate of plant size (shrub diameter).

In addition to damage, we counted the number of different species that caused damage on each leaf (or stem in the case of *Artemisia*). This measure allowed us to ask whether there were, on average, differences in the number of kinds of pathogens and herbivores present in the heated and control plots.

Statistics

Plot position, plot snowmelt date, and treatment are all likely to explain some of the variation in damage found in the experiment, but the three variables are themselves interrelated. The heating treatment primarily advanced the date of snowmelt (Fig. 1): On average, the heated plots melted out 10 d earlier than the control

plots (average day of year [day 1 = January 1] of 92 ± 3.8 vs. 102 ± 2.5 d). Melt date affects plant phenology, growth, and flowering success (Price and Waser 1998), which likely influence attack by herbivores and pathogens. However, these effects were complicated by plot position (Fig. 1). There is a natural gradient of melt dates across the slope; plots with more southern aspects melt out earlier than those with more northern aspects. Finally, plot position and treatment were related as all heated plots were one position further along the gradient.

Correlations among explanatory variables may cause their effects on host damage to be partially redundant, meaning that some of the variation in damage is attributable to two or more variables jointly (Whittaker 1984). The importance of these "shared effects" compared with the "unique effects" of each explanatory variable is likely to be different for each host species. Statistical models ignoring the possible redundancy among explanatory variables will lead to imprecise estimates of their effects (Zar 1996). We thus applied two different techniques to account for redundancy in our data set: variation partitioning and hierarchical ANCOVAs.

Variation partitioning was used to partial out the unique and the shared effects of our three explanatory variables. The procedure decomposes the total sum of squares (ss) of the dependent variable(s) into components that associated with each term of the model, plus an unexplained ("error") term. When the explanatory variables are redundant, the model ss consists of the ss explained by their unique effects, the ss explained by their shared effects, and the ss explained by their interactions (if included in the model). Note that (1) in our terminology, unique effects are the effect of one variable at a fixed level of the two other variables; (2) shared effects are not identical with interactions, the latter indicate that the effects of two explanatory variables influence each other, which can also occur if these variables are uncorrelated; (3) the total ss explained by two explanatory variables can be either the sum or the difference of the ss explained by their unique

TABLE 1. Procedure for variation partitioning using the damage calculations from *Artemisia tridentata* as an example.

Source of variation	Calculation	ss	Total ss (%)
Melt date	ss melt Model 1	0.00299	2.22
Treatment	ss treat Model 2	0.02773	20.58
Plot position	ss Model 1 – ss Model 3	0.01318	9.78
Shared melt date and treatment	ss melt Model 2 – ss melt Model 1	0.00494	3.66
Shared melt date and position	ss melt Model 3 – ss melt Model 1	0.05339	39.62
Shared treatment and position	ss treat Model 4 – ss treat Model 2	0.03655	27.12
Shared melt date and treatment and position	ss melt Model 4 – ss melt Model 3 – ss melt Model 2 + ss melt Model 1	–0.05019	–37.25
Model (all above)		0.08858	65.73
Error		0.04618	34.27
Total		0.13476	100.00

Notes: Individual and shared effects of three explanatory variables were calculated from the Type I sums of squares (ss) of four multiple regression models: (1) Position, Treatment, Melt date = damage; (2) Position, Melt date, Treatment = damage; (3) Treatment, Melt date = damage; (4) Melt date, Treatment = damage. See *Materials and Methods: Statistics* for a detailed explanation of the procedure.

and by their shared effects, respectively. It is the sum if unique and shared effects complement each other by acting in the same direction; it is the difference if they compete with each other by acting in opposite directions (Whittaker 1984).

Most ecological studies using variation partitioning have analyzed the responses of multispecies communities using canonical ordination models (Borcard et al. 1992, Anderson and Gribble 1998, Cushman and McGarigal 2002). We analyzed the responses of individual host species, and therefore used multiple regression models. We first calculated for each host species the mean fraction of tissue damaged and the mean number of attacking species in each plot. We then fitted a series of statistical models, from which we derived the ss associated with the unique and shared effects of the explanatory variables as shown in Table 1. Finally, each ss was divided by the total (model + error) ss to obtain the percentage of variation explained. Interaction effects were not included in the model but subsumed in the error term, because we did not have sufficient degrees of freedom to partial out their effects too, as we had data from only 10 plots.

To ask whether pathogens and herbivores differed in their response to the warming treatment, we used a hierarchical ANCOVA approach to separate the treatment effects on snowmelt from the position effects on snowmelt and their consequences for the percentage of tissue damaged. First, we ran ANCOVAs with the main effect of treatment plus the covariate snowmelt date to explain the percentage damage and the number of attackers (number of herbivores plus number of pathogens) present. The number of plants measured per plot (density) was used as a second covariate in all of the analyses of hosts for which we had censused all individuals (i.e., all but *Lathyrus*). This covariate was used because the experiment was erected over natural vegetation, and thus plots varied in the number of individuals of each plant species that were present. Note that in the decomposition of variation analysis, differ-

ences in plant density would have been included in the plot position variable.

Second, to remove the effect of plot position on snowmelt, we took the residuals from an ANOVA in which plot number and plot number squared (for non-linear effects) were the only factors. We then ran ANCOVAs on these residuals, with treatment as the main effect along with the covariates melt date and number of individuals per plot. To determine whether pathogens and herbivores responded similarly to the experiment, these analyses included a term for causal agent (pathogen or herbivore), and the interactions of causal agent with treatment and snowmelt date. Significant interaction terms indicate that pathogens and herbivores are not responding in the same way.

Data were transformed when necessary to meet the distribution and homogeneity assumptions of parametric analyses. All percentages were arcsine transformed, and when necessary, count data were either log or square-root transformed. We used the program JMP, version 5.0.1.2 (SAS 2003), for all analyses.

RESULTS

Did the heating treatment affect damage?

The heating treatment primarily influenced snowmelt date (Fig. 1). To determine the relative influences of treatment, plot position (aspect), and snowmelt date on damage, we decomposed the variation (Table 2A). The most consistent single factor that explained >5% of the variance in damage on most of the host species was snowmelt date (Fig. 2). Snowmelt date had its most significant effects through its shared influence on treatment and position, with up to 45.74% of the variance in the whole model being explained by the combined influence of treatment and snowmelt date. Treatment alone explained greater than 5% of the variation in damage for only one host species, *A. tridentata* (Table 2A). However, treatment had large (>10%) shared influence with melt date for two species (*H. quinque-*
nervis and *P. gracilis*) and large (>10%) shared influ-

TABLE 2. Partitioning of the total variation in host damage into components quantifying the unique and the shared effects of three explanatory variables as well as unexplained (error) variation: (A) percentage of tissue damaged, and (B) number of attacking species.

Source of variation	Total ss explained for each host species (%)					
	<i>Artemisia tridentata</i>	<i>Lathyrus leucanthus</i>	<i>Helianthella quinquenervis</i>	<i>Potentilla gracilis</i>	<i>Erigeron speciosus</i>	<i>Potentilla hippiana</i>
A) Percentage damaged						
Melt date	2.22	7.48	14.03	4.73	7.95	6.76
Treatment	20.58	1.93	5.96	0.66	1.25	5.72
Plot position	9.78	0.62	7.53	28.20	0.71	1.39
Shared melt date & treatment	3.66	20.12	45.74	10.35	0.28	-5.10
Shared melt date & position	39.62	22.53	-7.02	6.19	4.42	0.65
Shared treatment & position	27.12	-0.60	12.56	14.21	-0.59	-1.39
Shared melt date & treatment & position	-37.25	10.12	-10.41	-19.78	1.80	1.07
Model R^2	65.73	62.20	68.39	44.56	15.82	9.09
Error	34.27	37.80	31.61	55.40	84.18	90.91
Total	100.00	100.00	100.00	100.00	100.00	100.00
B) Number of attacking species						
Melt date	15.10	1.89	6.84	9.42	8.40	0.20
Treatment	13.15	6.16	5.52	0.06	4.54	10.91
Plot position	0.32	3.71	5.70	38.83	35.75	4.16
Shared melt date & treatment	-1.95	17.66	-5.02	7.39	-3.86	15.29
Shared melt date & position	35.01	20.50	47.21	-0.23	0.51	3.39
Shared treatment & position	6.70	-3.02	10.49	9.98	-3.78	13.08
Shared melt date & treatment & position	-17.85	13.15	-10.67	-14.63	4.51	-17.07
Model R^2	50.48	60.04	60.08	50.82	46.06	29.96
Error	49.52	39.96	39.92	49.18	53.94	70.04
Total	100.00	100.00	100.00	100.00	100.00	100.00

Notes: Shared effects are due to correlations among explanatory variables; negative signs for these effects indicate that they tend to compensate the unique effects, so that the total explained variation (model R^2) is smaller than it would be if explanatory variables were uncorrelated.

ence with position for three species (*A. tridentata*, *H. quinquenervis*, and *P. gracilis*). Plot position alone explained greater than 5% of the variance for three species, *A. tridentata*, *H. quinquenervis*, and *P. gracilis*. Of these, the effect of position on *P. gracilis* was the largest, with 28.20% of the variance explained by plot position alone. With the exception of *P. gracilis*, the largest influence of plot position was through its shared influence on the other variables.

Did the heating treatment affect the number of attacking species?

The heating treatment primarily influenced the number of attacking species by changing snowmelt date (Fig. 3, Table 2B). Treatment alone explained more of the variance in number of attackers than it did for damage (Table 2B). Treatment alone explained >5% of the variance in the number of attackers for *Lathyrus* and *Helianthella* and >10% for *Artemisia* and *P. hippiana*. Four of the six host species had >5% of the variation in attacker numbers accounted for by snowmelt date, and snowmelt date accounted for large amounts of the shared variation (Table 2B). Plot position was the most important single explanatory variable for the number of attackers on *P. gracilis* and *E. speciosus*.

Did herbivores and pathogens respond in similar ways?

Each host species was attacked by a combination of herbivores and fungal pathogens (Fig. 4), except for *Artemisia tridentata*, for which we only observed herbivores. The kinds of damage observed, and the associated causal agents are shown in Appendix A. One kind of damage, "mottling," we were unable to assign to a causal agent. It was found on three species (*H. quinquenervis* and the two *Potentilla* species). Mottling could have been an environmental response to drought, symptoms of a fungal or viral infection, or a response to herbivory. Since we were unable to determine the causal agent(s), we left this damage type out of the statistical analyses reported below. We do, however, illustrate mottling along with the other kinds of damage on the *Potentilla* species (e.g., Fig. 5C, D).

To determine whether pathogens and herbivores responded similarly to the heating treatment, we included a term for causal agent in the ANCOVA analyses (Table 3). There were always significant differences in the amount of pathogen and herbivore attack (significant "causal agent" effects), with herbivores causing more damage than pathogens on all the hosts except *Erigeron* (Fig. 4E).

Although there were differences in the amount of surface damage they caused, fungal pathogens and in-

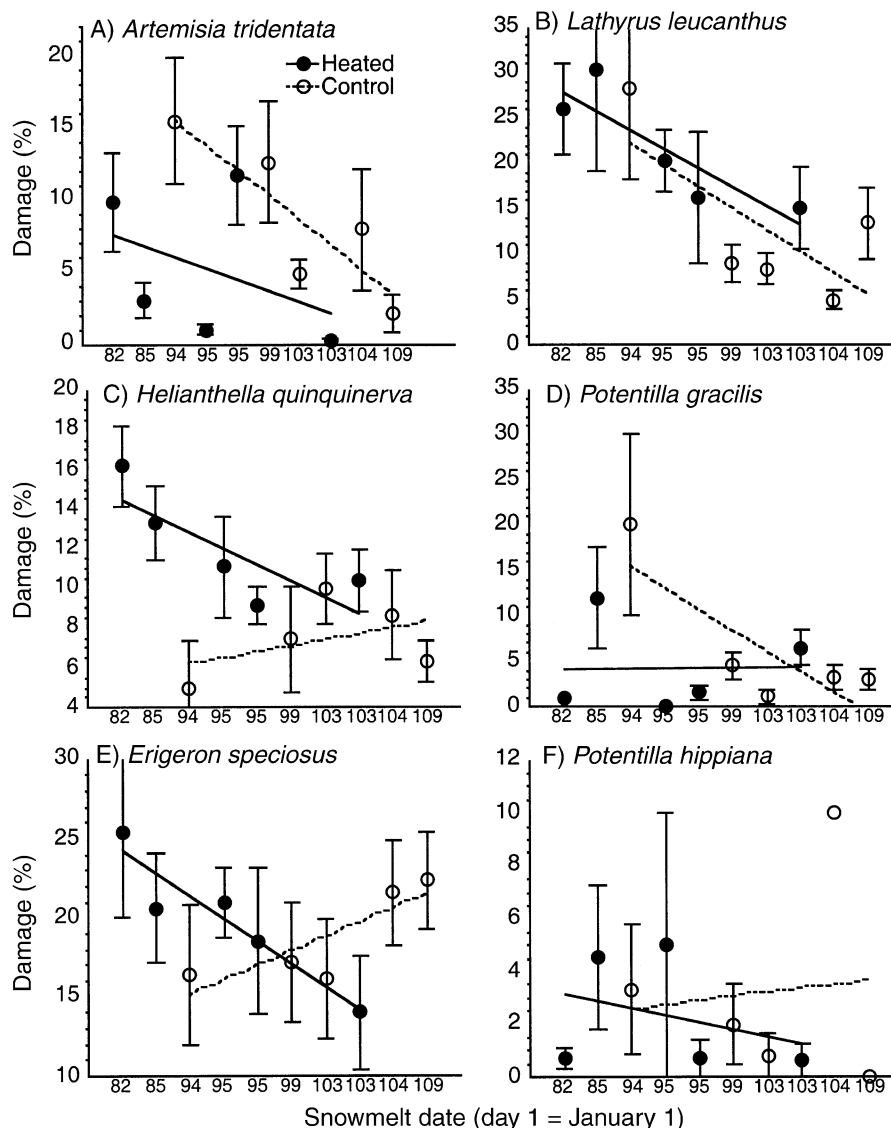


FIG. 2. Total damage (mean \pm 1 SE) to the six study species (i.e., damage caused by herbivores and pathogens added together; defined as the percentage of leaf area removed in all cases, except for *Artemisia*, where it is the percentage of stems showing damage), by treatment and snowmelt date (day of the year). The solid line is the regression for heated (treatment), and the dotted line is the regression for controls.

sect herbivores were, on average, similarly affected by the treatments as evidenced by a complete lack of significant interactions between causal agent and treatment for damage (Table 3). Although herbivores tended to show more of a response to melt date than the fungal pathogens did (Fig. 4), there was a significant interaction between damage and snowmelt date only for *L. leucanthus* (Table 3). For *L. leucanthus*, herbivore damage decreased with later melt dates, whereas pathogen damage remained about the same.

How did the heating treatment affect individual species of pathogens and herbivores?

Until now, we have discussed herbivores and pathogens as groups. It is valuable, however, to ask whether

individual species all responded similarly to the treatments. Each insect and pathogen species had its own microclimate preferences (Fig. 5). For example, there were four kinds of herbivores found on *A. tridentata* (Fig. 5A). Two tended to be more common in the controls: aphids (*Obtusicauda coweni* and *O. filifoliae*) and a stem-galling fly (*Rhopalomyia obovata*). Scale insects, on the other hand, were only found in the heated plots, and the fly causing leaf galls (*Rhopalomyia ampullaria*) showed no preference for either treatment.

For another example, we show the two species of *Potentilla* (Fig. 5C, D). The *Potentilla* species were attacked by the same species of pathogens and herbivores (see Appendix B), except there were no leaf min-

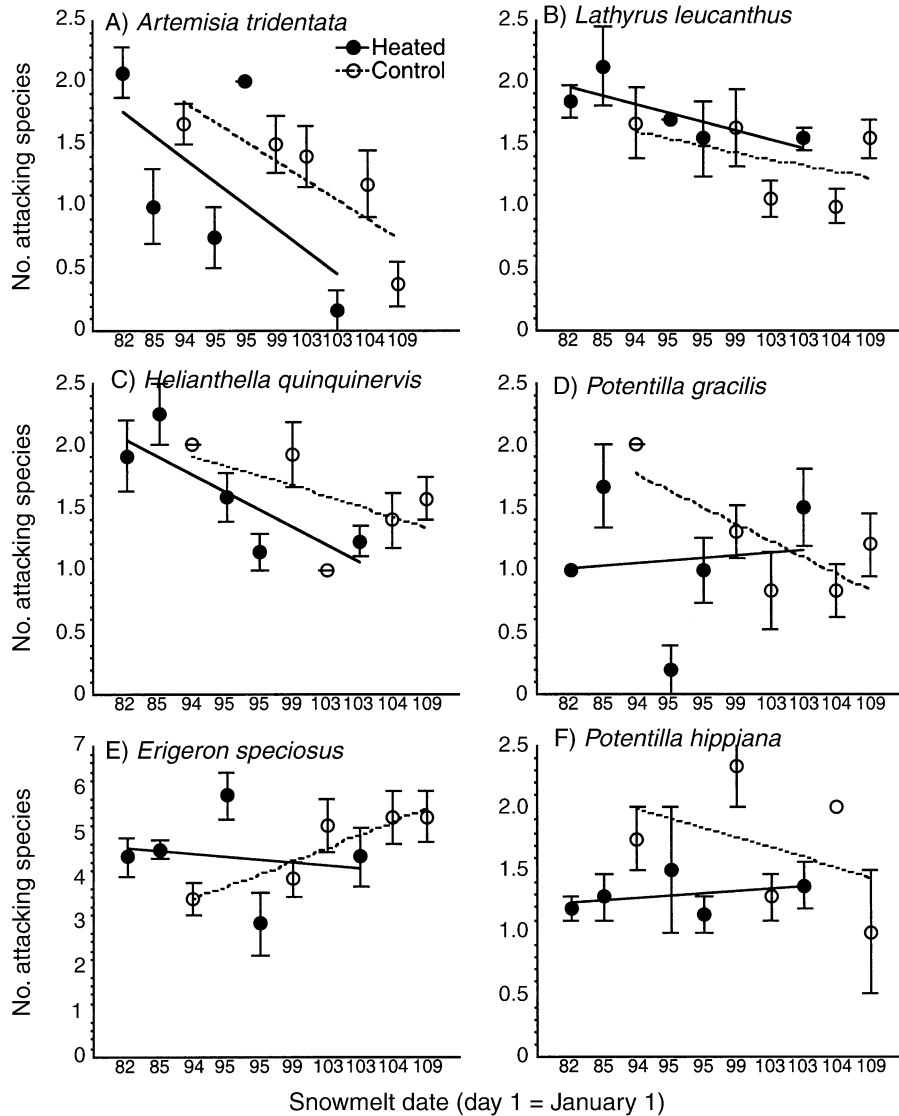


FIG. 3. Number of species of attackers (mean \pm 1 SE) of the six study species, by treatment and snowmelt date (day of the year). The solid line is the regression for heated (treatment), and the dotted line is the regression for controls.

ers on *P. hippiana*. However, the relative susceptibilities of the two *Potentilla* species differed. For example, *P. hippiana* was more susceptible to the rust fungus, *Phragmidium ivesiae*, and there was more mottling on *P. gracilis*. However, the different attacking species often showed similar responses to the treatments on both hosts: caterpillar rasping decreased in the heated plots, and chewing herbivore damage increased in the heating treatments. Due to large standard errors, none of the differences of individual species were significantly different between treatments except caterpillar rasping on *P. hippiana* ($P = 0.05$); however, melt date was often significant in these analyses. There was more damage in earlier melting plots for chewing and mottling on *P. hippiana*, and for caterpillar rasping and mottling on *P. gracilis*. Chewing was more com-

mon on *P. hippiana* in later melting plots (analyses not shown).

How did the heating treatment affect tritrophic interactions?

Not only did herbivores of *A. tridentata* respond to the treatments, but so did the species that depended on the herbivores. Aphids were more common in the control plots (Fig. 5A), thus it was not too surprising that their parasitoids were also more common in the control plots ($P < 0.0001$; Fig. 5B). Spiders were also significantly more common in the control plots ($P < 0.05$) and ants, which tended the aphids, were more common in the controls, but not significantly so (Fig. 5B).

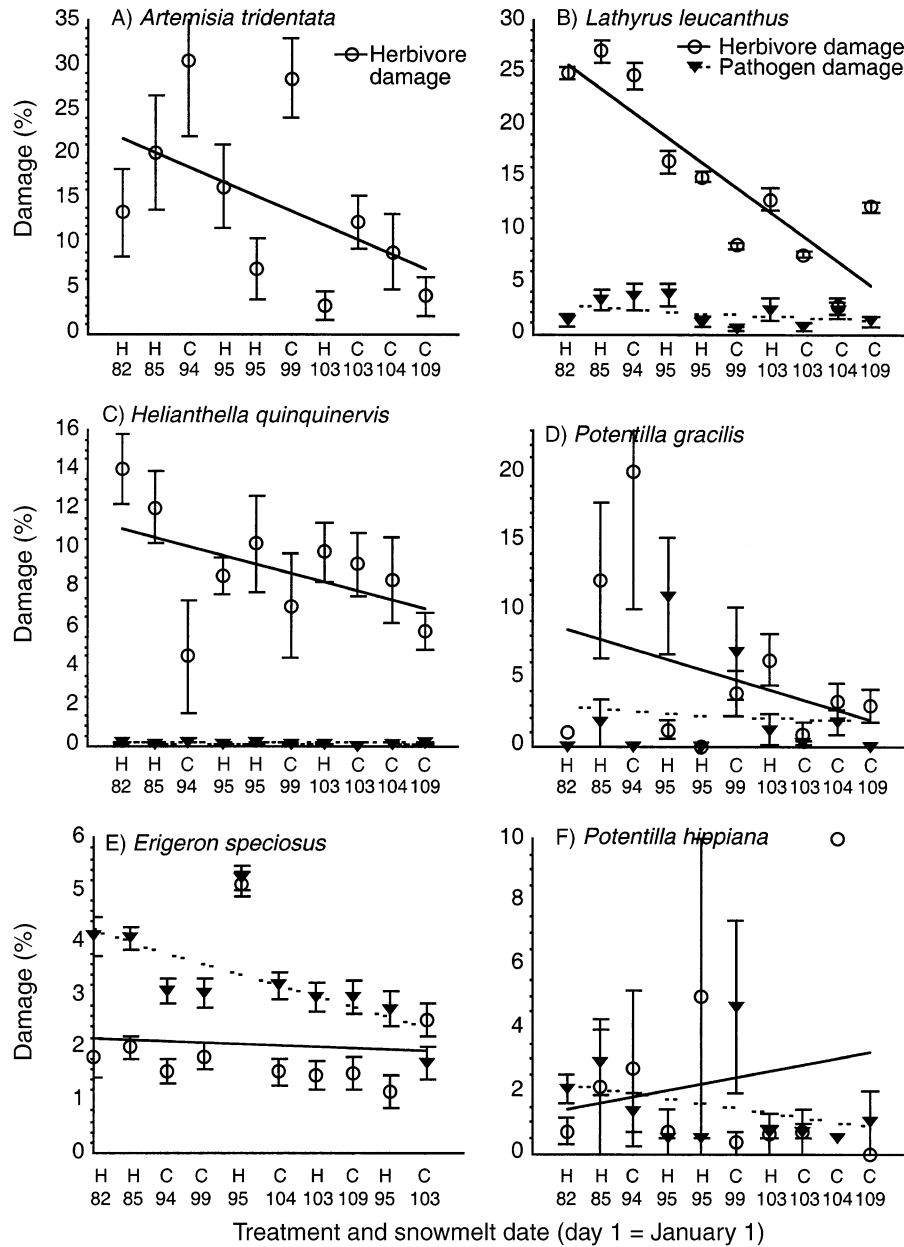


FIG. 4. Percentage of damage (mean \pm 1 SE) done by herbivores and pathogens to the six study species by treatment (H, heated; C, control) and snowmelt date (day of the year). The solid line is the regression for herbivore damage, and the dotted line is the regression for pathogen damage.

DISCUSSION

Insight from phenological gradients

Phenological differences can be used to gain insight into the effects of climate change (Parmesan and Yohe 2003, Root et al. 2003), and these differences can be particularly striking where snowmelt date sets up phenological patterns that persist through the growing season (Price and Waser 1998, Inouye et al. 2000, 2002, Root et al. 2003). We found that both the amount of

damage and the number of species of attackers tended to increase along a phenological gradient, with plants in earlier melting plots often having the most damage and the largest number of attackers (Figs. 2 and 3). These results are consistent with the prediction that pathogens and herbivores will tend to increase under the warmer conditions resulting from the current CO₂-driven climate change (Ayres 1993, Carter et al. 1996, Lonsdale and Gibbs 1996, Coakley et al. 1999, Ayres and Lombardero 2000, Malmström and Raffa 2000,

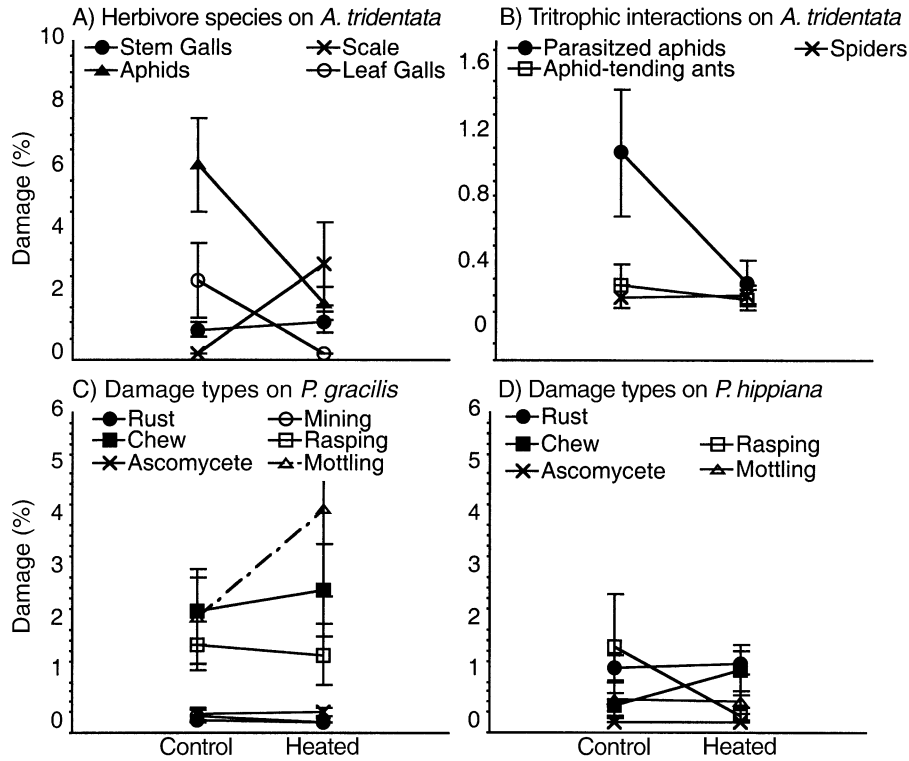


FIG. 5. Response of individual species of herbivores and pathogens to heating, shown as percentage of damage (mean \pm 1 SE) to three plant species. (A) Herbivores on *Artemisia tridentata*, (B) tritrophic interactions on *A. tridentata*, (C) herbivores and pathogens on *Potentilla gracilis*, and (D) herbivores and pathogens on *P. hippiana*. In all cases, the raw data are shown.

TABLE 3. Treatment and snowmelt date influences on damage as shown through ANCOVA: (A) treatment and snowmelt date effects on damage; (B) treatment and snowmelt date effects after removing plot position effects.

Effect	Host species					
	<i>Artemisia tridentata</i>	<i>Helianthella quinquenervis</i>	<i>Lathyrus leucanthus</i>	<i>Potentilla hippiana</i>	<i>Potentilla gracilis</i>	<i>Erigeron speciosus</i>
A) Treatment and snowmelt date effects on damage						
Treatment (treat)	0.0001+C	NS	NS	NS	NS	NS
Melt date (melt)	0.0001+E	0.05+E	0.05+E	0.05+L	NS	NS
Causal agent	Herbs only	0.0001	0.0001	0.001	0.0001	NS
Treat \times agent	...	NS	NS	NS	NS	NS
Melt \times agent	...	NS	<0.05	NS	NS	NS
No. plants/plot	0.001	NS	...	NS	NS	NS
Plant size	0.0001
Model R^2	0.46	0.78	0.34	0.15	0.30	0.02
B) Treatment and snowmelt influences on damage after removing plot position effects						
Treatment	0.0001+C	0.01+H	0.01+H	NS	NS	NS
Melt date	0.01+E	NS	NS	NS	NS	NS
Causal agent (agent)	Herbs only	0.0001	0.0001	0.001	0.0001	NS
Treat \times agent	...	NS	NS	NS	NS	NS
Melt \times agent	...	NS	0.05	NS	NS	NS
No. plants/plot	0.01	NS	NS	NS	NS	NS
Plant size	0.0001
Model R^2	0.39	0.79	0.33	0.13	0.32	0.02

Notes: Abbreviations for the direction of the effect: +C, more damage on controls; +H, more damage in heated plots; +E, more damage in earlier melting plots. Plant size was included as a covariate for *Artemisia tridentata*, but not for the other species.

Dale et al. 2001, Harvell et al. 2002) and constitute some of the first experimental measurements of pathogen responses to warming.

The climate change literature cited in the previous paragraph predicts that insects and pathogens will increase under warmer conditions because they will have longer growing seasons and thus will be able to complete more generations. An alternative mechanism for why damage tended to increase in early melting plots in our experiment is that insects simply gravitated to the sites that melted out first because food was present there earlier. In other words, because the scale of our experiment was small, the treatments tended to act as “choice tests” for the insects, who could choose to stay or leave. There is support for this hypothesis in our data set. Insects, which could move more than once, had a stronger response to both melt date and treatment than did the pathogens, which could not choose where to land (Fig. 4). To determine the exact mechanisms behind our results more experiments are needed, particularly those at larger spatial scales where choice of environments would be restricted.

Regardless of the exact mechanisms, our results indicate that where it snows, the date of snowmelt is a critical predictor for plant damage by herbivores and pathogens. Thus, experimental manipulations that seek to examine damage from herbivores and pathogens need to be certain that there is variation in snowmelt date. Some manipulations, such as small greenhouses erected each season after the snowmelt, as was recently done in Sweden (Richardson et al. 2002), will not affect snowmelt date. This may explain why there was no response by herbivores over the nine-year Swedish study.

Analysis of phenological gradients

We used two different kinds of analysis to disentangle the effects of snowmelt date, plot position, and the heating treatment: variation partitioning and hierarchical ANCOVAs. The decomposition of variation allowed us to determine that a large fraction of the variation in damage (or number of attacking species) was more the result of shared effects of treatment and position or melt date and position, and less the result of their independent effects. The hierarchical ANOVAs, on the other hand, removed all the effects of plot position, including any shared effects with melt date and treatment, yielding a conservative estimate of the effect of treatment beyond the plot position effects. The two kinds of analyses together give far more information than either alone. The decomposition clarifies where all the variance lies, including the shared effects, whereas the ANCOVAs clarify the influence of particular variables once the “nuisance variables” have been removed. In this particular data set, it is clear that plot position is more than a nuisance variable; it is part of what naturally influences snowmelt date, so it is important to understand this influence.

Plot position also influenced damage independently of its shared effect on snowmelt date. For example, in our data set, plot position explained a large fraction of the variation in damage and the number of attacking species on *P. gracilis* and *E. speciosus*. Why should this be? The variable “plot position” included in it variation as a result of plant density among plots, and all other factors that varied with spatial position. For example, if there is a moisture gradient across the slope, average plant size may also vary among plots. Larger experiments, with more degrees of freedom than our 10-plot means gave us, would allow further decomposition of the variance as a result of factors such as density and plant size.

Another benefit of the decomposition of variation was that it showed that the direction of shared effects could differ. For example, in Table 2A, there was a large negative term for the shared effects of melt&treatment&position on damage for *Artemisia tridentata* (−37.25). The negative term indicates that some factors had different effects on the data, which can also be seen by examining Figs. 2 and 3. For *Artemisia*, Fig. 2A shows that the warmed plots had less damage, but that earlier melting plots (which were also warmer) had more damage. The effect of plot position is not illustrated, but the key effects we were interested in were snowmelt date and the effects of treatment on snowmelt date.

Idiosyncratic species responses

A major result from our study was that damage patterns varied among the host species (Fig. 2), and the herbivores and pathogens also varied in their responses to environmental conditions (Figs. 4 and 5). Although there were usually more herbivores and pathogens in plots that melted out earlier, sometimes there were more in later melting plots (Fig. 4). The presence of idiosyncratic species responses such as those shown in Fig. 5 is important because it suggests that individual species will not necessarily all respond in the same way to climate change, and thus, that the species composition of communities will change. Rather than the same host–parasite community being reassembled at higher latitudes or elevations, it is more likely that species frequencies will shift, with some taxa becoming more common, others being added, and others dropping out. In addition, changing environmental conditions are likely to lead to situations in which hosts come into contact with novel pathogens and herbivores; a circumstance that often favors epidemics (Weste 1981, 1986, Hiers and Evans 1997, Harvell et al. 2002).

We found more aphids on *Artemisia tridentata* in control plots, even after the effects of snowmelt date and plot position had been accounted for. This tendency for aphids to prefer *Artemisia* in the control plots was consistent with two of the three years of data collected from 1996 to 1998 in the same experimental plots (P. de Valpine and L. Adler, *personal communication*).

They found that, not only were a higher proportion of stems infested in the control plots, there were more aphids per stalk, and aphid population growth rates were higher on the control plants. We suspect that the reason the aphids preferred plants in the control plots was because of the drying effects of the heaters. However, further experimentation is necessary to determine the reason(s) for their preference.

To date, there has been little research on the effects of climate change on parasitoids and predators (Simberloff 2000). Our results with the associates of aphids (Fig. 5B) suggest that these organisms are likely to mirror the preferences of their hosts. What is not yet known is whether climate affects tritrophic interactions directly, or whether these organisms are simply responding to the population sizes and preferences of their hosts. It would also be interesting to determine whether the increase of parasitism of aphids in the control plots (where aphids were most abundant) ultimately reduces the amount of damage caused by aphids to the level found in the heated plots.

Most of the plants in our study had more damage from herbivores than by pathogens. This does not mean that pathogens are less important; however, because they also usually grow internally and they often produce toxins (Agrios 1997). Our heating treatment caused changes in temperature and associated changes in plant phenology and plant characteristics (Harte and Shaw 1995, Loik and Harte 1996, 1997, Price and Wasser 1998, De Valpine and Harte 2001), as well as soil drying and other biogeochemical changes (Torn and Harte 1995, Shaw and Harte 2001, Saleska et al. 2002). While some regions will certainly see more drought, other regions will experience increases in both precipitation and humidity (IPCC 2001), which will strongly affect spore production and infection by fungal pathogens (Coakley et al. 1999). Studies of pathogens are needed in which temperature, rainfall, and humidity are manipulated.

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APPENDIX A

A table listing damage types and identity of the attackers of all hosts is available in ESA's Electronic Data Archive: *Ecological Archives* E085-075-A1.

APPENDIX B

A figure showing herbivore and pathogen damage on *Potentilla gracilis* is available in ESA's Electronic Data Archive: *Ecological Archives* E085-075-A2.