



Article Will Climate Warming Alter Biotic Stresses in Wild Lowbush Blueberries?

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Abstract: As global temperatures rise, a growing need exists for understanding the impacts of warming on crop production. Warming not only changes crop physiology and growth but also the weeds, insect pests, and diseases of crops including wild lowbush blueberries, which have not been studied till now. Changes in pest pressures can cause instability in production and will require changes in management practices and the development of mitigation strategies. The objective of this study was to determine the impacts of warming on the prevalence of major weeds, insect pests, and diseases of the wild blueberry production system. We selected six genotypes of wild lowbush blueberries in a commercially managed wild blueberry field in Maine Northeast USA and used open-top-chambers (OTCs) to study the effects of warming for two years (2019 and 2020). Both active-heating OTCs (elevated monthly mean temperatures by 3.3 °C) and passive-heating OTCs (elevated by 1.2 °C) were employed and compared with ambient controls. Our results showed that warming did not change the prevalence of red leaf disease, blueberry gall midge, red-striped fireworm, or any weed species. In contrast, the incidence of Sphaerulina leaf spot, powdery mildew, and other leaf spot disease were significantly lower under warming treatments compared to the ambient control at the end of the growing season in 2020. Overall, different pests responded to warming differently, inviting further research to reveal the mechanisms. The lower overall pressure of leaf spot disease under warming was probably due to decreased air humidity.

Keywords: climate change; global warming; wild blueberry; insect pests; pathogens; diseases; weeds

1. Introduction

Anthropogenic climate change challenges both natural plants and crops [1,2]. The global land surface temperature has increased by 0.14 °C per decade from 1880 to 2020 [3]. Based on the historical trend and model predictions, the global average surface temperature will increase by 1.7 to 4.8 °C by 2100 [4]. In Maine, the average annual air temperature has increased by 1.8 °C during the past 124 years and is predicted to increase further by 2 to 6 °C (3 to 9 °F) by 2100 [5]. Elevated temperatures can change the growth rhythm (phenology) of crop plants [2], and impact the incidence of insect pests, diseases, and weeds in agricultural systems [6]. However, the impacts of warming on biotic stresses are less studied than on the performance of plants. Because wild lowbush blueberry fields in Maine warm faster than other landscapes in the region [7], they may be exposed to a greater threat and warrant the need for research that assesses the potential impacts of warming.

As important factors determining crop yield and early indicators of climate change, insect pests, pathogens, and weeds are sensitive to climate change [6,8]. Warming is expected to affect the regional incidence of insects, pathogens, and weeds, thus raising production costs because of adjustments in farming practices and increased application of



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). agrochemical controls [9]. Additionally, the effects of a changing climate make pest and pathogen attacks more unpredictable in a greater magnitude [10–12], potentially resulting in greater fluctuations in crop yields [13]. Thus, climate change may cause an increase in the frequency or intensity of disturbances in outbreaks of insect pests [4,14]. As insects are cold-blooded and sensitive to temperature changes, higher temperatures can increase the development rate of insect pests and reduce the time between generations [9]. Global warming is also driving the active movement and consequently expanding the range of pests towards the poles [15]. Additionally, warming affects the development and survival of pathogens, disease transmission, and host susceptibility [11], and may increase the frequency of disease outbreaks. For example, because warming extends the growing season, slightly warmer temperatures in combination with humid conditions will increase the incidence of late blight in the future [16]. Although most crops experience more frequent or severe disease impacts under warming, some pathogens may be reduced with warming, allowing hosts to mitigate the stress from diseases [17].

Warming may also affect weeds, which can reduce crop growth mainly by competing with the crops for resources. When weeds do not actively compete with the crop, weeds can still interfere with the wild blueberry harvest through weed seed and plant material contamination impacting the marketability of the berries [18]. Weeds alone significantly reduce crop performance by an average of 28%, and the combined effects of weeds and environmental change reduce crop yield by 27% [19]. Climate warming will alter the balance of competition between crops and weed species. Generally, weeds can be more competitive under climate change compared to crops due to their stronger ability to adjust the ratio of root to shoot growth [20], as well as in increasing maximum biomass [9]. Thus, warming can lead to an increase in weed pressure in the field [21].

The wild blueberry production system is a unique semi-natural agricultural system with high genetic and physiological diversity in the field (Figure 1). Wild, or lowbush blueberries, are deciduous woody perennials native to North America. They naturally grow on acidic soils (pH 4–5) and can tolerate a soil pH level as low as 2.5 [22]. They can be found on any soil type in the understorey of forests but grow optimally in well-drained soils [23,24]. Naturally growing wild blueberry plants, mainly *Vaccinium angustifolium* Aiton and *Vaccinium myrtilloides* Michx. [25,26] are commercially managed to form a carpet of plants (Figure 1) for berry production in Maine USA and the Maritime provinces and Quebec in Canada [27]. A two-year crop scheme has been adopted for the management of commercial wild blueberries in the field, where berries are produced and harvested in fields every second year [28]. The aboveground vegetation is pruned by burning or mowing after harvest to create a prune year (year one) and then a crop year (year two).

Pest management is important in wild blueberry production, and integrated pest management has contributed greatly to increased yields in Maine [29]. In 1980, the application of the herbicides terbacil and hexazinone distinctly reduced weed competition with wild blueberry crops, which doubled yields. The most common foliar diseases of wild blueberries include a variety of leaf spot diseases, including Sphaerulina leaf spot (Sphaerulina vaccinii, old name Septoria), powdery mildew (Erysiphe vaccinii Schwein), and leaf rust (Thekopsora minima (Arthur) Syd. & Syd) [29,30], which affect both prune and crop year plants but their effects on yield are difficult to assess as they are usually found in combination [30]. Another foliar disease, red leaf (Exobasidium vaccinii (Fuckel) Woronin), also weakens wild blueberries and reduces fruit production, lowering the number of flowers per stem by 42% and the number of berries by 74% [31,32]. Secondly, the most common native insect pests in Maine wild blueberries fields are blueberry gall midge (Dasineura oxycoccana Johnson), blueberry spanworm (Itame argillacearia Packard), blueberry fea beetle (Altica sylvia Malloch), the blueberry thrips complex (Frankliniella vaccinii Morgan, Catinathrips vaccinophilus Hood, and Catinathrips kainos O'Neill), blueberry maggot fly (*Rhagoletes mendax* Curran), and grasshoppers of many species (primarily *Melanopus* spp.). These pests are directly or indirectly related to yield variation [33–37]. Another pest, the red-striped fireworm (Aroga trialbamaculella Cham.) has not been documented

to cause economic yield losses to blueberries but is a nuisance pest that interferes with harvest [31] The only serious exotic insect pest of Maine wild blueberries is the spotted wing drosophila, *Drosophila suzukii* Matsumura [38]. This pest does cause economic crop loss in wild blueberry [39]. Third, weed infestation by a variety of woody and herbaceous weeds reduces fruit quality and is one of the stresses for limiting the yield of wild blueberries [29,35,38,40]. The weed flora of wild blueberry fields is unique, consisting mainly of a wide range of native herbaceous and woody perennial species that thrive under a two-year cropping cycle [41]. The most common weed is Bunchberry (*Cornus canadensis* L.), which readily competes with blueberries and reduces the quality of berries due to the presence of orange-red berries as contaminants during harvest. The second most common weed is Colonial bentgrass (*Agrostis capillaris* L.) [42].



Figure 1. High crop morphological diversity of a wild blueberry field at the Blueberry Hill Research Farm in Jonesboro, Maine USA. Different genotypes were indicated by phenotypic differences in leaf and stem colours. Photo credit: Xiaoxue Mo.

The wild blueberry is one of the most important crops in Maine USA, which produces 99% of wild blueberries in the USA and 40% of all wild blueberries around the globe [43]. However, the total production and the average yield per area have been decreasing in the last six years [44]. The reduction in yield could be related to climate change, which has not been assessed, as well as economic factors. While the wild blueberry production system is resilient to climate change because of the high genetic variability within fields, the crop is not immune to global warming [43,45]. Also, wild blueberry fields are experiencing a faster rate of warming compared to the adjacent regions in Maine [7]. The impacts of warming on its weeds, insect pests, and diseases have not been studied till now. The objective of this study was to determine the impacts of warming on the severity of common biotic stresses in the wild blueberry system including weeds, insect pests, and plant diseases. We used open-top chambers (OTC) in the field to simulate climate warming. Our hypothesis was that experimental warming will increase pest pressure due to increased activity and development rate of insects, and greater pathogen incidence due to greater dispersal on warm air currents possessing higher entropy and faster pathogen development rates in warmer environments. We also hypothesized that warming would decrease weed incidence because wild blueberry crops are regarded as highly resistant to environmental stresses and would perform physiologically better compared to weeds under elevated heat stress.

2. Materials and Methods

2.1. Study Site

The experiment was conducted at Blueberry Hill Research Farm (67.6° N, 44.6° W) in Jonesboro, Washington County, Maine USA from May 2019 to September 2020. The average annual temperature was 6.4 °C in 2019 and 7.8 °C in 2020, while annual precipitation was 1432 mm in 2019 and 952 mm in 2020 [3]. The soil in which the experiment was conducted is Colton gravelly sandy loam with a pH of 4.7 [46]. The field was pruned in 2018, and thus it was in the prune (vegetative growth, year one) phase/stage in 2019, and crop (berry production) phase/stage in 2020.

2.2. Experimental Design and Treatments

A randomized block design was used for this study. Six different genotypes of wild blueberries (V. angustifolium) were designated as six blocks. Six genotypes were chosen based on their morphological and physiological characteristics to represent the field crop genetic diversity. Within each block (genotype), plants were randomly assigned to treatments. Three different levels of experimental warming were deployed including an active-heating (AH) open-top chamber (OTC) with a heating tape, a passive-heating (PH) OTC without a heating tape, and an ambient control group without a chamber and a heating tape (CON), were randomly assigned within each genotype, except for two genotypes with only two levels of treatments due to the limited land area they covered. Therefore, four out of the six genotypes had one AH, one PH, and one CON treatment. For the other two genotypes, one had AH and CON treatments, while the other had PH and CON treatments. The OTCs were constructed with LEXAN polycarbonate sheets (glass substitute) of the following dimensions: 3 mm thickness with a 100 cm base, 70 cm top, and 55 cm sides cut at an angle of 60° [45,47]. For the AH OTCs, a 12-m-long waterproof silicone heating tape with a 240 W power rating (Briskheat, Columbus, OH, USA) was coiled around a hexagon of metal tubing and attached to the inside the OTC at a height of 15 cm [45]. WatchDog 1000 Series Micro Stations (Spectrum Technologies Inc., Aurora, IL, USA) were installed in the centre of four AH, four PH, and two CON treatment plots, and recorded air temperature and relative humidity every 30 min.

2.3. Pest Rating

The weed, disease, and insect pest pressures were rated based on their prevalence, which were visually estimated based on their symptoms (Figure 2) and ranked from 0 to 5 within a 0.09 m² (0.3 m × 0.3 m) sampling quadrat, where: 0 = not present, $1 = \leq 20\%$, 2 = 20-40%, 3 = 40-60%, 4 = 60-80%, 5 = 80-100%. The broadleaf weed and grassy weed observations were treated as a single category of weeds. For overall leaf spot disease, the percentage of powdery mildew, Sphaerulina leaf spot, and leaf rust incidences were pooled and treated as a single category of leaf spot [48]. The insect pest observations of incidence were based on the symptoms of infestation on leaves for the blueberry gall midge and the red-striped fireworm [36,49]. The percentage of leaves infested was rated visually on a rank scale. The rating ranked from 0–5 (0 = not present, $1 = \leq 20\%$, 2 = 20-40%, 3 = 40-60%, 4 = 60-80%, 5 = 80-100%) in each plot. No other insect pests were observed colonizing the experimental plots. The weed and insect pest, infestation measurements were conducted on 27 June, 11 July, 28 July, 11 August, 24 August, and 9 September in 2019, and 14 June, 2 July, and 11 August in 2020.

To further separate the pressure of different leaf and stem diseases, a more detailed field study was carried out once each year at the end of the growing season. The percentage prevalence of Sphaerulina leaf spot, powdery mildew, leaf rust, and *Phomopsis* twig blight were determined separately based on their symptoms (Figure 2) in a 0.25 m \times 0.25 m area within each plot on 21 August in 2019, and 28 August in 2020, respectively.

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Figure 2. Symptoms of major diseases and insect pests in the wild lowbush blueberry field investigated in the present study. The photos show the typical symptoms of (**a**) red leaf disease, (**b**) Sphaerulina leaf spot disease, (**c**) powdery mildew, (**d**) *Phomopsis* twig blight, (**e**) blueberry gall midge, and (**f**) red-striped fireworm. Photos were taken in the field by Seanna Annis (**a**–**d**) and Lily Calderwood (**e**,**f**).

2.4. Statistical Analysis

Data were analysed using the SPSS software (version 25, IBM Corp., Armonk, NY, USA). Homogeneity and normality of the variance were tested, and data were log-transformed if needed. Two-way analyses of variance (ANOVA, $\alpha = 0.05$ and $\alpha = 0.01$) were performed on each of the weed, insect pest, and disease measures (dependent variables) to statistically test the effects of the three temperature treatments with the genotype as the random factor and treatment (active-heating OTC, passive heating OTCs, and control) as the fixed factor. For post-hoc analyses, the pest incidence means were compared by the least significant difference (LSD) test at 95% confidence. If the results reached the significant level ($\alpha \le 0.05$), the treatment means were presented by including the other two genotypes of blueberries with two levels of treatment. Graphs were then constructed as visual aids for interpreting the fixed effects.

3. Results

During the prune year 2019 from May to October, the mean monthly atmospheric temperature of the AH chambers was 3.8 °C higher than the CON (Figure 3a). The mean monthly atmospheric temperature of the PH chambers was 1.6 °C higher compared to that of the CON plots (Figure 3a). In 2020 (April to August), the mean monthly atmospheric temperature of the AH was 2.89 °C higher than for the ambient controls (Figure 3b). The mean monthly atmospheric temperature of the passive heating (PH) chambers was 0.75 °C higher compared to that of the controls (Figure 3b). Meanwhile, the relative humidity was lower in the AH and PH chambers compared to the controls. In 2019, the mean monthly relative humidity was 10.1% lower in the AH chambers than that in the CON and 1.82% lower in the PH chambers than in the CON (Figure 3c). In 2020, the mean monthly relative humidity was 9.83% lower in the AH chambers than that in the CON and 1.49% lower in the PH chambers than in the control (Figure 3d).

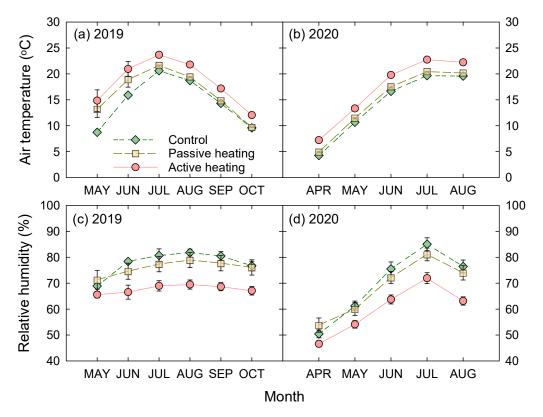


Figure 3. Mean monthly atmospheric temperatures in 2019 (**a**) and 2020 (**b**), as well as mean relative humidity in 2019 (**c**) and 2020 (**d**) of different treatments. Green diamonds denote the ambient control plots (CON), yellow squares are passive-heating (PH) open-top-chambers (OTCs), while red circulars indicate the and active-heating (AH) OTCs. The values are means \pm SEs (four weather stations in the AH and PH chambers and two weather stations in the CON).

No significant differences in overall leaf spot disease among different treatments were found in 2019, a prune year (Figure 4a). No red leaf disease was detected in any treatments in 2019 (Figure 4c). In 2020, a crop year, the leaf spot disease ratings of wild blueberry plants in the AH chambers were significantly lower (56%) compared to the ambient control on 24 August (236 DOY) (Figure 4b). No differences were detected in the prevalence of overall leaf spot disease in June and July (Figure 4b). Also, no significant difference in red leaf disease was detected between the treatments in 2020 (Figure 4d).

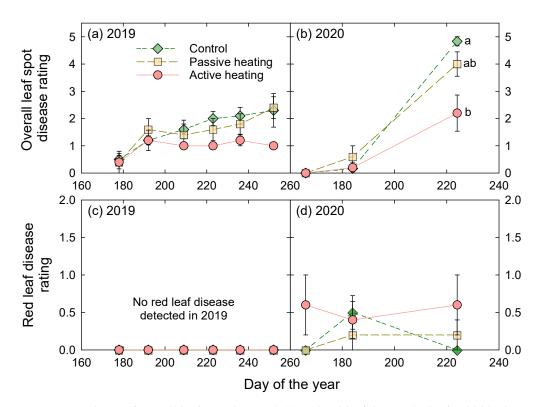


Figure 4. Incidence of overall leaf spot disease (**a**,**b**) and red leaf disease (**c**,**d**) of wild blueberries under different treatments in 2019 (prune year; **a**,**c**) and 2020 (crop year; **b**,**d**). The rating ranked from 0–5 (0 = not present, $1 = \leq 20\%$, 2 = 20-40%, 3 = 40-60%, 4 = 60-80%, 5 = 80-100%) of the control plots (CON), passive-heating OTCs (PH) and active-heating OTCs (AH). Data are means \pm SEs. Green diamonds with dashed lines denote the ambient control plots (CON), yellow squares with dashed lines are passive heating (PH) OTCs, while the red circulars with solid lines indicate the active heating (AH) OTCs. The absence of letters or points with the same letter indicate treatments that do not differ significantly (*p* > 0.05).

At the end of the growing season of 2019, the percent infection of wild blueberries by Sphaerulina leaf spot disease under the AH treatment was significantly lower compared to the control and PH treatment, but no differences were detected between plants in the control and the PH treatment (Figure 5a). At the end of the growing season in 2020, the percent infection by Sphaerulina leaf spot disease of wild blueberries under the AH treatment was significantly lower compared to the control, but no differences were detected between the control and PH treatment (Figure 5b). No significant difference in powdery mildew was detected among different treatments in 2019 (Figure 5c). However, in 2020, the percent infection of powdery mildew was significantly lower on plants in the AH treatment compared to the control (Figure 5d). No leaf rust was detected under any of the treatments. *Phomopsis* twig blight was only detected in wild blueberry plants under the AH treatment in both 2019 and 2020 (Figure 5e,f) but at low percentages (0.08% in 2019 and 0.7% in 2020).

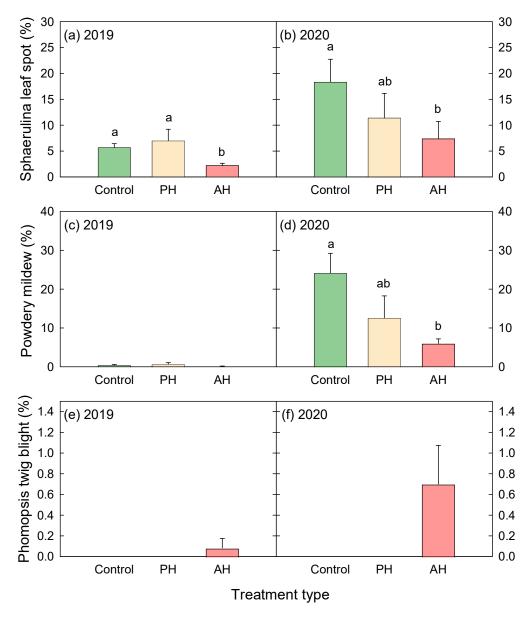


Figure 5. Warming impact on pathogen diseases. The percentage infection of Sphaerulina leaf spot disease (**a**,**b**), powdery mildew (**c**,**d**), and *Phomopsis* twig blight (**e**,**f**) of wild blueberries under different treatments in 2019 and 2020 at the end of the growing season (21 August 2019 and 28 August 2020). Different treatments are controls, active-heating (AH), and passive-heating (PH) chambers. Bars are means + SEs. The absence of letters or bars with the same letter do not differ significantly among treatments (*p* > 0.05).

No difference in the incidence of blueberry gall midge, and red-striped fireworm were found among the treatments throughout the growing season in 2019 and 2020 (Figure 6). In both years, the red-striped fireworm tended to increase over time (Figure 6c,d). In addition, no difference in the incidence of weeds was detected among the treatments throughout the season in both 2019 and 2020 (Figure 7).

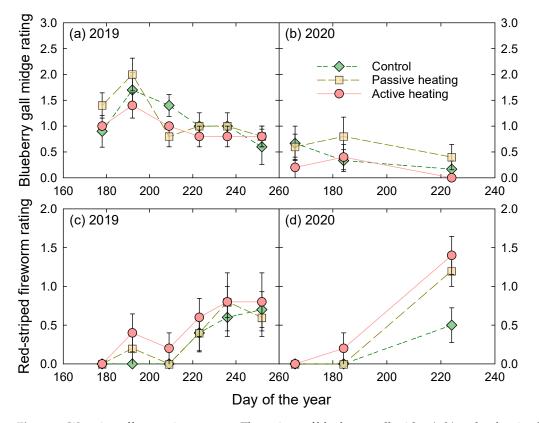


Figure 6. Warming effects on insect pests. The ratings of blueberry gall midge (**a**,**b**) and red-striped fireworm (**c**,**d**) of wild blueberries under different treatments in 2019 (prune year; **a**,**c**) and 2020 (crop year; **b**,**d**). The rating ranked from 0–5 (0 = not present, $1 = \le 20\%$, 2 = 20-40%, 3 = 40-60%, 4 = 60-80%, 5 = 80-100%) of the control plots (CON), passive-heating OTCs (PH) and active-heating OTCs (AH). Data are means \pm SEs. Green diamonds with short dashed lines denote the ambient control plots (CON), yellow squares with long dashed lines are PH OTCs, while red circulars with solid lines indicate the AH OTCs. The absence of letters indicates treatments that do not differ significantly (p > 0.05).

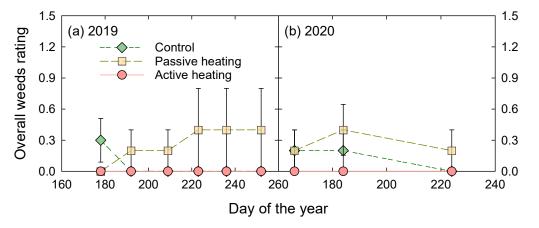


Figure 7. Warming impact on weeds. The incidence of overall weeds of the wild blueberry fields under different treatments in 2019 the prune year (**a**), and in 2020 the crop year (**b**). Data are means \pm SEs. Green diamonds with short dashed lines denote the ambient control plots (CON), yellow squares with long dashed lines are passive-heating (PH) OTCs, while red circulars with solid lines indicate the active-heating (AH) OTCs. No significant differences were detected among the treatments (*p* > 0.05).

4. Discussion

Our results provide evidence that climate warming may change biotic stresses in agricultural systems [6]. Warming differentially affected weeds, insect pests, and diseases in the wild blueberry system. Overall, warming of 1.2 °C had a limited impact on all the pests, suggesting that the wild blueberry production system is relatively stable under relatively small increases in temperature. However, warming of 3.3 °C altered the infection of leaf spot diseases and may have affected the presence of stem twig blight. A temperature elevation of 3.3 °C is an intermediate value predicted to happen at the end of this century in Maine [5]. In contrast, warming did not alter the prevalence of weeds and insect pests. As weed establishment takes time, further studies over a longer-term are needed to investigate the competition between weeds and wild blueberry crops. Significantly lower levels of leaf spot disease in both the vegetative growth phase and fruit production phase under warming of 3.3 °C suggest a potential benefit brought by warming in the wild blueberry system. However, Phomopsis stem blight was only found under the active warming treatment (AH), suggesting this may be a negative impact of warming. As pest management is an important factor determining the yield of wild blueberries [29], changes in pest pressure can potentially affect growth and yield [35].

Decreased overall leaf spot diseases, and Sphaerulina leaf spot, and powdery mildew, in particular, could be due to decreased atmospheric humidity under the warming treatments (Figure 2c,d). Survival, reproduction, and transmission of pathogens are greatly influenced by both atmospheric temperature and humidity (for a review, see [50]). Increased temperatures can increase the survival, development, reproduction, and transmission of pathogens [17]. The fungi causing both diseases overwinter on plant material and so higher temperatures would affect the production of inoculum as well as plant development and likely would not put the fungus out of sync with its host for infection. Thus, the inhibiting effect in the warming OTC might be related to decreased relative humidity associated with warming-induced water loss rather than warming itself. High atmospheric humidity greatly enhances the virulence of diseases and promotes their infection on plant tissues [50]. In the wild blueberry production system, the pathogen infection is also greatly dependent on relative humidity [51–53]. Thus, a decrease in relative humidity due to warming most likely inhibited leaf spot pathogen infection in the wild blueberry.

Different pathogen diseases may respond differently to warming [17]. While leaf spot diseases were lower under warming treatments, no difference in red leaf disease was detected among treatments and stem blight was only found under the active warming treatment (AH). For red leaf disease, the pathogen infects stems and gets established in the rhizomes of wild blueberries. Thus, it can last several years in the infected stems, and a longer-term study is probably needed to detect the impacts of warming on its development. For stem blight, temperature rather than humidity could be the dominant factor in influencing pathogen development and infection. Warming could have promoted the survival and infection of the stem blight pathogen, as commonly found in other pathogens [50].

In terms of the dynamics of disease incidence, no differences in overall leaf spot disease were detected at the early stage of the plant and fruit development (sprouting and fruit set in 2020 the crop year, Figure 4b), but this is typically when plants are being infected by these leaf spot diseases. Leaf spot symptoms are first visible in early June and worsen over the growing season. Thus, the effect of warming could be cumulative over the season and occur during spore dispersal and while new infections are produced (powdery mildew and leaf rust) or as lesions worsen and expand as is seen with all the leaf spot diseases. *Thekopsora minima*, the leaf rust fungus, first infects eastern hemlock (*Tsuga canadensis*) in the spring and then spores are blown onto blueberry plants. The chambers may have affected the dispersal of this pathogen, though no leaf rust was found on the controls without chambers.

Our expected increase in insect pests under the warming treatment was not supported by the results. Higher temperatures can increase the rate of development of insect pests and reduce the time required for reproduction [9]. However, no differences were detected among different treatments in the present study. Notably, almost all of the insect pests in the wild blueberry production system, except the spotted wing drosophila, are native insect pests. Therefore, it might be that these native insect pests are adapted to lower air temperatures that have been associated with thousands of years of blueberry growth in Maine [34], and their rate of development may not increase with warming. Additionally, in this study, the chambers may have partly blocked the movement of insects, which needs to be considered in interpreting the data.

Weeds studied here in the wild blueberry production system were not sensitive to warming. Notably, the chambers may have blocked the weed seed dispersal in our experiment, partly influencing the pattern for warming impacts on weeds. However, chambers would not have affected the existing seed bank density at the initial start of the experiment. In addition, because weeds present in the wild blueberry production system are mostly perennials, a longer-term study is needed to investigate their establishment and competition with the wild blueberry crop plants under climate change.

5. Conclusions

In conclusion, climate warming may have both positive and negative impacts on biotic stresses in the wild blueberry production system. The two common leaf diseases in the system, Sphaerulina leaf spot and powdery mildew seem to be inhibited by warming, probably due to the warming-induced decrease in relative humidity. The development and infection of Sphaerulina leaf spot is sensitive to changes in wetness and germination and infection of spores is highly reliant on high air relative humidity. As Northeast USA is predicted to be drier in the future [54], the pressure of these two diseases may decrease. In contrast, other diseases, such as red leaf, may not be that sensitive to warming and changes in humidity. The presence of *Phomopsis* twig blight only in the active warming treatment warrants further study of the effect of warming on this disease. Different responses of different diseases to warming suggest changes in disease infection patterns in the future, which may require adjustments in pest management. Additionally, warming of 3.3 °C seems to have a limited impact on current insect pests and weeds. Further, warming may promote the movement and activity of novel invasive pests and weeds [15,55], which need to be considered in planning and policymaking. While our study provides a first look at the warming impacts on the pest complex in the wild blueberry production system, further detailed studies on different pests are needed to reveal physiological mechanisms regulating their responses. How these changes in pest pressure will impact crop growth and yield should also be studied.

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Data Availability Statement: All data are available upon request from one of the corresponding authors (yongjiang.zhang@maine.edu).

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