High temperature and soil moisture reduce host-plant quality for an insect herbivore

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Abstract. 1. Anthropogenic climate change is a substantial threat to global biodiversity. It may affect insect herbivores directly and indirectly. Indirect effects are, among others, mediated by climate-change induced variation in host-plant quality. Although being potentially important, little is known on the significance of such indirect effects and on interactions among environmental stressors in plant–herbivore interactions.

2. To simulate the potential impact of climate change, we investigated effects of host-plant temperature and soil moisture on herbivore performance in the tropical butterfly *Bicyclus anynana* under laboratory conditions.

3. Maize grown at high temperatures or under wet conditions reduced herbivore performance, indicated by decreased body mass, storage reserves, phenoloxidase activity, and increased development time. Temperature and soil moisture acted largely independent of one another. Detrimental effects of the high plant temperature were restricted to males, indicating a higher vulnerability of this sex to environmental stress.

4. In nature, *B. anynana* might be threatened by increasing temperatures during the wet season negatively affecting host-plant quality. Our study shows that herbivore performance can be substantially affected by indirect effects mediated through changes in host-plant quality, which deserves more attention in the current era of global climate change.

Key words. climate change, environmental stress, indirect effect, interactive effect, plant–insect interaction, water deficit.

Introduction

Human impact is all pervasive and currently changing the Earth's ecosystems at an unprecedented rate (Maxwell *et al.*, 2016; Díaz *et al.*, 2019). Among the various anthropogenic threats to biodiversity, climate change has received particular attention in recent years (e.g. Hansen *et al.*, 2012; Pecl *et al.*, 2017). This is likely because its wide-ranging consequences are becoming ever more evident, having already resulted in changes in community composition as well as phenological and range shifts in a broad array of species (Scheffers *et al.*, 2016; Stillman, 2019). Future climate change is predicted to comprise a substantial challenge to extant biodiversity, which may cause a global mass extinction (Foden *et al.*, 2013; Keith *et al.*, 2014). During the course of climate change, temperature and precipitation patterns are changing, increasing the risk of

heat and drought stress for many organisms including plants and their herbivores (Rahmstorf & Coumou, 2011; Hansen *et al.*, 2012; Harvey *et al.*, 2020).

Much research has been dedicated to understanding the direct consequences of variation in temperature and soil moisture on plants and animals (e.g. Bale *et al.*, 2002; Pelini *et al.*, 2009; Ahuja *et al.*, 2010; Reyer *et al.*, 2013). Our knowledge on the potential role of indirect as well as interactive effects though is still limited (DeLucia *et al.*, 2012; Jamieson *et al.*, 2017; Decker *et al.*, 2018, 2019). Indirect effects arise if the effect of an environmental factor is mediated via another variable or organism. For instance, changing environmental conditions will yield direct effects on both plants and herbivores. If these affect the plant's chemical composition and thereby its nutritional quality for the herbivores, the latter will be additionally affected by indirect effects mediated via their host plants (Pelini *et al.*, 2009; Bauerfeind & Fischer, 2013a, 2013b). Interactive effects are important as multiple stressors typically act jointly in complex ecosystems (Qaderi *et al.*, 2006; Ahuja *et al.*, 2010; Mundim & Bruna, 2016; Jamieson *et al.*, 2017).

Because of their inability to escape from unsuitable environments, plants have evolved a wide spectrum of mechanisms to protect themselves against changing conditions (e.g. Fernandes *et al.*, 2008; Shulaev *et al.*, 2008; Ramírez *et al.*, 2009; Theocharis *et al.*, 2012). Among different environmental stressors, drought and elevated temperatures seem to have the strongest impact on plants (Ahuja *et al.*, 2010). Elevated temperatures increase transpiration rates causing water loss due to a vapor pressure deficit, as is the case during droughts (Ohashi *et al.*, 2006; Chapman *et al.*, 2012). Water deficits decrease photosynthesis activity caused by stomatal closure (Qaderi *et al.*, 2006; Zhang *et al.*, 2014). This in turn results in shifts of carbon and nitrogen content and allocation, reducing growth in favour of survival and protection against (drought) damage (Gutbrodt *et al.*, 2011). For instance, plants may contain less nitrogen when grown under elevated temperature, at least in combination with elevated carbon dioxide levels (Zvereva & Kozlov, 2006; DeLucia *et al.*, 2012). Stress-induced changes in plant chemistry, e.g. in allelochemicals, may also compromise defenses against herbivores (Friberg & Wiklund, 2016).

Just as plants, insect herbivores are also affected by direct effects of environmental stress and variation. Higher temperatures increase developmental rates and heat tolerance, but decrease body mass and the efficiency of converting food into body matter (Ayres & Lombardero, 2000; Hoffmann *et al.*, 2002; Fischer & Karl, 2010; Harvey *et al.*, 2020). Drought stress is known to reduce insect activity, growth, and body mass (Scherber *et al.*, 2013). However, insect herbivores are additionally affected by indirect effects mediated by changes in the plants' chemical composition (Price, 2002; Hunter, 2003; DeLucia *et al.*, 2012). Feeding on plants grown at high temperature, for instance, decreased larval growth rates and reduced body mass and the efficiency of converting food into body matter in butterflies (Awmack & Leather, 2002; Hwang *et al.*, 2008; Bauerfeind & Fischer, 2013a). This may be causally related to a low leaf nitrogen content (Tabashnik, 1982; Ravenscroft, 1994) or an enhanced leaf toughness making them more difficult to process (Coley, 1983; Floater, 1997). Drought stress, on the other hand, may actually increase host-plant quality for herbivores, as evidenced by increased body mass and growth rate, potentially through a reduced investment into plant defense mechanisms (Larsson, 1989; Gutbrodt *et al.*, 2011; Franzke & Reinhold, 2011; Bauerfeind & Fischer, 2013b; Salgado & Saastamoinen, 2019).

In summary, insect herbivores are likely to be affected by indirect effects of climate change, mediated via their host plants. We here investigate the consequences of host-plant manipulations on herbivore performance in the tropical butterfly *Bicyclus anynana* (Butler, 1879). We used two important stressors playing a crucial role in current anthropogenic climate change, temperature, and soil moisture, to manipulate host plants. Both factors are particularly relevant in our study system, as *B. anynana* inhabits highly seasonal environments with a cool-dry and a wet-warm season (Brakefield, 1997; Lyytinen *et al.*, 2004). Moreover, investigating tropical ectotherms is of great importance as they are particularly threatened through climate change (Deutsch *et al.*, 2008). We hypothesise that plants grown under (1) higher temperature (due to a higher C:N ratio) and (2) wet conditions (due to increased investment into defense against herbivores) will reduce herbivore performance. We further predict (3) both factors to interact in a way that, overall, plants grown under cool and dry conditions comprise highest food quality. Finally, we hypothesise that (4) males will be more strongly affected by poor host-plant quality than females. This assumption rests on the fact that male butterflies, including *B. anynana*, show intrinsically higher growth rates than females, making them more vulnerable to environmental stress (Fischer & Fiedler, 2000; Salgado & Saastamoinen, 2019). To assess herbivore performance, we scored development time, morphology, and two physiological traits indicative of condition. Overall, this study aims at unravelling indirect effects of simulated climate change on the performance of a herbivorous insect.

Material and methods

Study organism

Bicyclus anynana is a fruit-feeding butterfly ranging from Ethiopia to Southern Africa (Larsen, 1991). This species shows two seasonal morphs, which is thought to function as an adaptation to alternate wet-dry seasonal environments and the associated changes in resting background (Brakefield, 1997; Lyytinen *et al.*, 2004). Individuals having developed during the colder dry season (May until November) have fairly uniform wing patterns and small eyespots, while those having developed in the warmer wet season show large eyespots and bright bands on both wings (December until April; Larsen, 1991; Lyytinen *et al.*, 2004). Reproduction is confined to the warmer wet season, when oviposition plants are abundantly available (Brakefield, 1997). The animals used in this experiment came from the laboratory stock population of Greifswald University, which was established from the stock population at Leiden University. The Leiden population was founded in 1988 from 80 gravid females caught at a single locality in Malawi. In each generation, several hundred individuals are reared to maintain high levels of heterozygosity at neutral loci (Van't Hof *et al.*, 2005).

Experimental design

Maize plants (*Zea mays* L.) for larval feeding were grown under different conditions potentially affecting host-plant quality. We used two temperature and two water regimes, resulting in four treatment groups: (1) 19 °C, wet (150 ml of water per watering day); (2) 19 °C, dry (50 ml per watering day); (3) 25 °C, wet; (4) 25 °C, dry. All plants were reared at constant temperatures in climate cabinets (Sanyo MLR-351H) in plastic pots (11 x 11 x 12 cm; 8–10 plants per pot; 60 pots per treatment) using commercially available potting soil. They were watered every other day. Plants grown under 'wet' conditions received enough water to keep them turgid throughout, while plants grown under 'dry' conditions showed temporarily signs of wilting. Plants were not fertilised throughout.

For larval rearing, ca. 600 eggs were collected from the stock and kept at 26 °C until hatching. Afterwards, larvae were randomly divided among the four host-plant treatments (100 larvae per treatment). All larvae were reared in groups of five in small plastic boxes (125 ml) at 26 °C, 70% relative humidity, and a L18:D6 photoperiod. These conditions mimic summer conditions and are used by default in our laboratory, ensuring high survival of animals. They were fed *ad libitum* with leaf cuttings of the respective treatment until pupation. Boxes were checked daily and supplied with fresh leaves as necessary. Resulting pupae were collected and kept individually until eclosion. After adult eclosion, butterflies were frozen at −80 °C for further analyses. Development time was recorded from the day of hatching until the day of adult eclosion. All animals used in this study were wet-season phenotype.

To assess effects of host-plant treatments, we measured several morphological and physiological parameters. First, total body mass of frozen butterflies was determined to the nearest 0.01 mg (Sartorius CPA225D). Then, wings, head, and legs were removed. Thorax and abdomen were separated and afterward weighed. Thorax-abdomen ratio was calculated as thorax divided by abdomen mass. Forewing length and area were measured using digital images of left forewings. Images were captured from ventrally with a digital camera mounted on a stereo microscope and analysed with NIS elements software. Wing loading was calculated as total body mass divided by forewing area, and wing aspect ratio as 4 x forewing length^2 divided by forewing area (Berwaerts *et al.*, 2002).

Abdomen fat content was measured following Fischer *et al.* (2003), but using acetone instead of dichloromethane. In short, abdomens were first dried to constant weight for 2 days at 70 °C and dry mass was measured. Afterwards, fat was extracted twice for 2 days each, using 2×1.5 ml of acetone for each butterfly. Then, abdomens were dried again for 2 days and the fat-free dry mass was measured. Relative fat content was determined as the mass difference between initial and remaining dry mass after fat extractions and is given in percent.

Phenoloxidase (PO) activity was used as a representative of the insect immune system and as an indicator of general condition (González-Santoyo & Córdoba-Aguilar, 2012; Bauerfeind & Fischer, 2014). For PO measurements, thoraces were homogenised (Tissuelyser II, Qiagen; 15 s at 30 Hz) with 200 μl of a phosphate buffered saline (PBS) and afterwards centrifuged for 10 min at 14 000 rpm. Afterwards, 60 μl of the supernatant or of PBS buffer (for blank measurements) was transferred to a microtiter plate (96-well). Then, 140 μl L-Dopa (dihydrophenyl-L-alanine; 10 mM in PBS buffer) was added. Readings were taken every 30 s on a spectrophotometric plate reader (BioTek EL 808) at 30 °C and 490 nm for 45 min. Enzyme activity was measured as the slope during the linear phase of the reaction, during which the enzyme catalyses the transition from L-Dopa to dopachrome. PO activity was assayed twice per individual and controlled for blank values. The mean of both readings was used for statistical analyses. Total protein content was quantified using the Roti Nanoquant protein assay based on the Bradford method (Bradford, 1976), according to the manufacturer's instructions (Roth, Germany).

Statistical analyses

All statistical tests were performed using Statistica 12.0 (Statsoft, 2003). Data were analysed with general linear models (GLMs) using host-plant temperature, host-plant water regime, butterfly sex and all two- and three-way interactions as fixed factors. We considered additionally including 'box' as a random or blocking factor, however, the effect could not be estimated due to empty cells and collinearity. Protein content was added as covariate when analysing PO activity. We used the Levene and the Kolmogorov−Smirnov test to explore homogeneity of variances and normal distribution of residuals. Minimum adequate models were constructed by sequentially removing non-significant interaction terms. We verified our models by using an AIC approach, giving in all cases the same result. To locate significant differences among treatments, Tukey HSD post hoc tests were used. All means are given ± SE.

Results

Out of the 10 traits measured, plant temperature significantly affected development time, total body mass, thorax mass, wing loading (i.e. total mass divided by wing area), and relative fat content (Table 1). Feeding on plants grown at the higher temperature increased development time by ca. 2 days (though only in combination with wet conditions, significant temperature by water interaction), but decreased total body mass by ca. 8%, thorax mass by ca. 5%, wing loading by ca. 10%, and relative fat content by ca. 18% (Fig. 1, Supplementary Table S1). Additionally, PO activity tended to be lower when having fed on plants from 25 °C than from 19 °C. This difference was significant under dry conditions (significant temperature by water interaction).

Plant water regime significantly affected development time, forewing area, and wing aspect ratio. Feeding on plants grown under dry compared to wet conditions decreased development time by ca. 2.3 days (though only at 25 °C, significant temperature by water interaction), reduced wing aspect ratio indicating rounder, less elongated wings under dry conditions, but increased forewing area by ca. 4%. In addition, relative fat content tended to decrease when having fed on plants from dryer conditions.

Butterfly sex significantly influenced all traits measured (Table 1). Females compared to males showed longer development times, higher total body, thorax and abdomen masses, lower thorax-abdomen ratios, larger wings, higher wing loadings, lower wing aspect ratios indicating rounder wings, higher PO activities, and lower relative fat contents.

These general patterns though were partly modulated by interactive effects (Table 1). Significant interactions between plant temperature and sex were found for development time, total body mass, thorax mass, abdomen mass, thorax-abdomen ratio, forewing area, and PO activity. Males reared on plants grown at 19 °C had significantly shorter development times compared to males reared on plants gown at 25 °C, while females did not exhibit a difference (Tukey HSD after GLM). Likewise, effects of plant temperature on total body and thorax mass were restricted to males, being reduced when feeding on

Table 1. Results of general linear models for the effects of host-plant temperature (19 vs. 25 °C), host-plant water regime (wet vs. dry), and butterfly sex on various traits in *Bicyclus anynana*

	Beta ± SE	MS	DF	F	P
Development time					
Temperature	−0.281 ± 0.051	265.7	1, 275	30.51	**<0.0001**
Water	0.315 ± 0.052	315.9	1, 275	36.28	**<0.0001**
Sex	−0.274 ± 0.051	249.1	1, 275	28.60	**<0.0001**
Temp. × Water	−0.456 ± 0.053	694.7	1, 275	74.60	**<0.0001**
Temp. × Sex	−0.115 ± 0.051	43.5	1, 275	4.99	**0.0216**
Error		8.7	275		
Total body mass					
Temperature	0.114 ± 0.052	794.0	1, 276	4.84	**0.0287**
Water	−0.046 ± 0.052	124.6	1, 276	0.76	0.3843
Sex	−0.517 ± 0.054	15246	1, 276	92.89	**<0.0001**
Temp. × Sex	0.137 ± 0.053	1091.2	1, 276	6.65	**0.0104**
Error		164.1	276		
Thorax mass					
Temperature	0.122 ± 0.050	60.2	1, 276	6.02	**0.0147**
Water	−0.065 ± 0.050	17.1	1, 276	1.71	0.1919
Sex	−0.573 ± 0.051	1254.0	1, 276	125.40	**<0.0001**
Temp. × Sex	0.105 ± 0.051	43.1	1, 276	4.30	**0.0388**
Error		10	276		
Abdomen mass					
Temperature	0.033 ± 0.042	14.9	1, 276	0.60	0.4397
Water	−0.059 ± 0.043	47.3	1, 276	1.90	0.1696
Sex	−0.727 ± 0.044	6885.0	1, 276	276.04	**<0.0001**
Temp. × Sex	0.144 ± 0.043	273.9	1, 276	10.98	**0.0010**
Error		24.9	276		
Thorax-abdomen ratio					
Temperature	0.039 ± 0.042	0.01	1, 276	0.88	0.7850
Water	0.049 ± 0.042	0.02	1, 276	1.38	0.8799
Sex	0.738 ± 0.043	3.75	1, 276	295.49	**<0.0001**
Temp. × Sex	−0.120 ± 0.043	0.01	1, 276	7.99	**0.0051**
Error		0.01	276		
Forewing area					
Temperature	−0.012 ± 0.046	32	1, 272	0.07	0.7944
Water	−0.100 ± 0.047	2131	1, 272	4.54	**0.0340**
Sex	−0.652 ± 0.048	86360	1, 272	184.04	**<0.0001**
Temp. × Sex	0.159 ± 0.048	5240	1, 272	11.17	**0.0009**
Error		469	272		
Wing loading					
Temperature	0.210 ± 0.058	0.048	1, 273	12.99	**0.0004**
Water	0.036 ± 0.059	0.001	1, 273	0.38	0.5371
Sex	−0.205 ± 0.058	0.045	1, 273	12.28	**0.0005**
Error		0.004	273		
Wing aspect ratio					
Temperature	−0.008 ± 0.055	<0.01	1, 273	<0.01	0.8863
Water	0.117 ± 0.056	0.42	1, 273	4.40	**0.0366**
Sex	0.392 ± 0.055	4.72	1, 273	50.20	**<0.0001**
Error		0.09	273		
Fat content %					
Temperature	0.221 ± 0.051	816.0	1, 276	18.87	**<0.0001**
Water	0.094 ± 0.051	146.0	1, 276	3.37	0.0637
Sex	0.471 ± 0.051	3701.1	1, 276	85.56	**<0.0001**
Error		43.3	276		
Phenoloxidase activity					
Temperature	0.114 ± 0.063	1125.1	1, 253	3.33	0.0692
Water	0.052 ± 0.064	222.9	1, 253	0.66	0.4175
Sex	−0.137 ± 0.064	1540.6	1, 253	4.56	**0.0337**
Temp. × Water	−0.145 ± 0.066	1645.2	1, 253	4.87	**0.0282**
Temp. × Sex	0.159 ± 0.064	2097.4	1, 253	6.21	**0.0134**
Water × Sex	−0.163 ± 0.062	2372.9	1, 253	7.02	**0.0086**
Protein	0.019 ± 0.061	30.9	1, 253	0.09	0.7625
Error		337.9	253		

Protein content was added as covariate for phenoloxidase activity. Models were constructed by sequentially removing non-significant interaction terms. Significant *P*-values are given in bold.
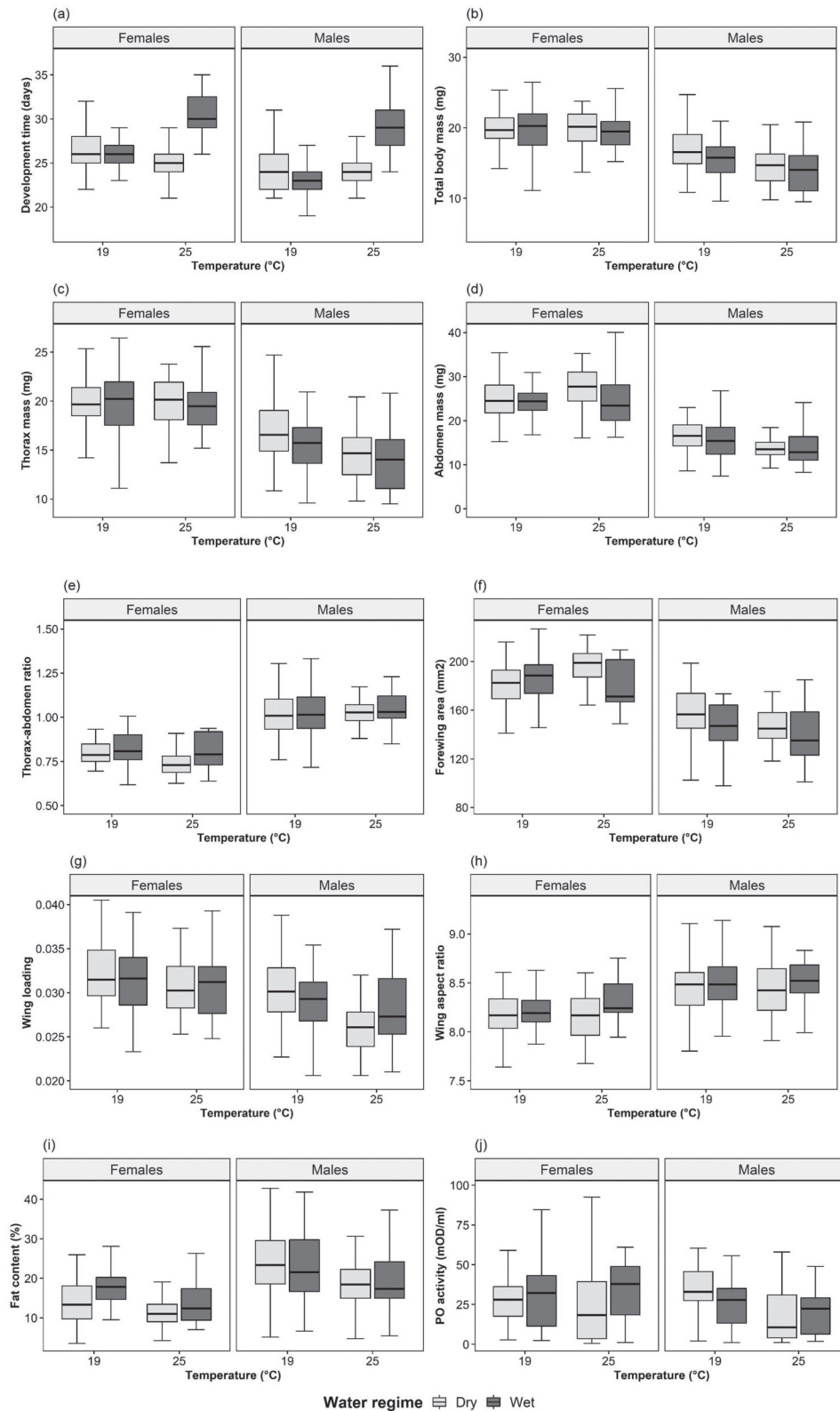
Fig. 1. Effects of host-plant temperature (19 vs. 25 °C), host-plant water regime (wet vs. dry), and butterfly sex on development time (a), total body mass (b), thorax mass (c), abdomen mass (d), thorax-abdomen ratio (e), forewing area (f), wing loading (g), wing aspect ratio (h), fat content (i), and phenoloxidase activity (j) in *Bicyclus anynana*. Given are medians (thick lines), interquartile ranges (boxes), and highest and lowest values (whiskers).

plants from the higher temperature (Tukey HSD). For abdomen mass and wing area, the higher plant temperature tended to reduce values in males but to increase in females, resulting in a much more pronounced sex difference at 25 °C. The reverse pattern was found for thorax-abdomen ratio. For PO activity, effects of plant temperature were once again restricted to males, being lower when reared on plants from the higher temperature (Tukey HSD). Thus, all seven plant temperature by sex interactions show that exclusively males were negatively affected by plants from the higher temperature, while the females remained unaffected throughout. Finally, a significant plant water regime by sex interaction was found for PO activity only, indicating that values increased when fed with plants from dry conditions in males but decreased in females. Three-way interactions were non-significant throughout.

Discussion

Our study examined the responses of the herbivore *B. anynana* to variation in temperature and water regime of its host plant *Z. mays*. As expected, high temperature and wet conditions altered host-plant quality and thereby reduced herbivore performance. Note that the quality of host plants is assessed only from the performance of butterflies, and is not based on direct measurements of plant chemistry.

Temperature indirectly affected various aspects of insect herbivore performance. In line with hypothesis 1, we found that the higher growing temperature reduced host-plant quality by decreasing the herbivore's body mass, wing loading, relative fat content, and PO activity (only under dry conditions), and by increasing development time, similar to some earlier studies (Buse *et al.*, 1998; Bauerfeind & Fischer, 2013a). Reduced body mass, storage reserves, PO activity as well as longer development times clearly indicate diminished insect performance in *B. anynana* (Karl *et al.*, 2011; Fischer *et al.*, 2014). Such detrimental effects may be causally related to decreased foliage nitrogen content and a concomitantly increased C/N ratio (Buse *et al.*, 1998), with nitrogen often being a key determinant of herbivore performance (Mattson, 1980; Zvereva & Kozlov, 2006). Bauerfeind & Fischer (2013a) further showed increased food intake, i.e. compensatory feeding, on low-quality host-plants grown at elevated temperatures, which is a common mechanism to alleviate effects of reduced nutrient availability. Additionally, higher temperatures may increase the concentration of secondary metabolites such as terpenes (defense compounds in maize against herbivory; Yatagai *et al.*, 1995; Block *et al.*, 2019) and leaf toughness and thus diminish digestibility (Coley, 1983; Buse *et al.*, 1998; Meihls *et al.*, 2012).

Detrimental effects of plants grown under wet conditions on herbivore performance were found in line with hypothesis 2, namely, through decreased fat content (non-significant), forewing area and thus body size, but increased development time. The significance of an increased wing aspect ratio under wetter plant conditions is difficult to assess, as changes in wing shape have both advantages and disadvantages, and because the functional relationships between flight morphology and flight performance are not fully understood in butterflies (Gibbs

et al., 2012). Nevertheless, decreased body size and storage reserves in combination with a prolonged development time testify reduced herbivore performance on plants exposed to wet conditions. Similar results pointing towards an increased host-plant quality of drought-stressed plants were also found in other studies (Larsson, 1989; Gutbrodt *et al.*, 2011; Bauerfeind & Fischer, 2013b; Salgado & Saastamoinen, 2019). However, drought may also have negative effects on herbivore performance, indicating that responses vary among species, developmental stages, and the intensity of drought stress (e.g. Huberty & Denno, 2004; Mody *et al.*, 2009; Scherber *et al.*, 2013; Salgado & Saastamoinen, 2019).

With regard to our third hypothesis, we found only limited support for strong interactions among environmental factors. Only two out of 10 traits were affected by temperature by water interactions, showing that development time was only prolonged when feeding on plants from the high temperature and wet conditions, and that PO activity was only reduced when feeding on plants from the high temperature and dry conditions. Though modulating some traits, interactive effects were clearly less pronounced than expected, indicating that high temperature and drought stress may affect plants largely independently.

Sexes of *B. anynana* differed in all traits measured. Females were larger and had a higher PO activity than males, while males developed faster, had higher thorax-abdomen and wing aspect ratios and a higher relative fat content. These differences reflect well-known patterns present in many insect species, resulting from differential selective pressures (e.g. Gilchrist, 1990; van Dyck & Wiklund, 2002; Merckx & van Dyck, 2005; Berwaerts *et al.*, 2006). To increase mating opportunities, males are selected for early emergence (protandry) and high flight ability (Wiklund & Fagerstrom, 1977; Karl & Fischer, 2008). In contrast, females develop longer and achieve higher body masses due to fecundity selection (Honěk, 1993; Blanckenhorn, 2000). More interestingly, males were indeed more strongly affected by poor host-plant quality than females (hypothesis 4), but only in relation to temperature. In fact, plant temperature by sex interactions were significant for seven out of 10 traits, all showing that males suffered from feeding on plants grown at the higher temperature while the females did not. The males' higher vulnerability to environmental stress may be due to their rapid life style (Fischer & Fiedler, 2000; Salgado & Saastamoinen, 2019). However, why this was not also found in relation to water availability is unclear. We assume that temperature and drought stress may affect plants largely independently and impose differential responses (see also above), and that effects of temperature may be stronger than those of drought, at least under the conditions used in our study. We also cannot rule out that traits other than the ones measured here are additionally affected. Thus, future studies should also investigate reproductive performance, which might be compromised by poor food quality especially in females.

In summary, our results indicate that temperature and water availability profoundly affected maize plant quality for the insect herbivore *B. anynana*. Plants grown at a high temperature or under wet conditions reduced herbivore performance, but did so largely independently. Detrimental effects of the high plant temperature were largely restricted to males. In nature,

B. anynana occurs in regions of Africa with two distinct seasons, a warmer wet and a cooler dry season. As development is largely restricted to the wet season with 2–3 generations (Larsen, 1991), the species seems to be vulnerable to increasing temperatures negatively affecting host-plant quality. Reduced rainfalls during the wet season, on the other hand, will likely have less severe and perhaps even positive impacts. Our study shows that herbivore performance may be diminished by indirect effects mediated through changes in host-plant quality, a topic which deserves more attention in the current era of global climate change.

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Author contributions

JK and KF designed the experiments, JK collected the data, JK, AR and KF analysed the data, JK, AR and KF wrote the manuscript.

Conflict of interest

The authors declare that they have no conflicts of interest.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon request.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Effects of host-plant temperature, host-plant water regime, and butterfly sex on various traits in *Bicyclus anynana*.

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