Environmental Research Letters

LETTER

Contrasting yield responses of winter and spring wheat to temperature rise in China

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Keywords: global warming, active growth duration, yield component, artificial warming, phenology, climate change

Abstract

Wheat growth, development, and grain yield are affected by global climate warming. The general consensus is that global warming shortens the overall length of wheat growing period and reduces global wheat yield. Here, focusing on China, the largest wheat producer in the world, we show that warming increases wheat yield in most winter wheat growing regions in China. We collated data from field experiments under stress-free conditions and artificial warming from 12 locations over China to assess the impact of warming on wheat yield. The data cover 14 wheat cultivars, 27 site-years, and a range of growing season temperatures from 7.5 °C to 17.2 °C. Our results indicate that warming up to +3 °C increased winter wheat yield by 5.8% per °C (change rate of yield/average of yield), while reduced spring wheat yield by 16.1% per °C. Although artificial warming reduced the total growth duration, warming-induced longer early developmental phases and grain filling duration, and subsequently more and larger grains contributed to the yield increase of winter wheat. The yield decline of spring wheat was due to the opposite changes of those key processes in response to temperature rise.

1. Introduction

Accelerated anthropogenic global climate changes, most notably in spatial and temporal temperature patterns, have been observed since the mid-20th century (Fang et al. 2015, Zhao et al. 2016). Global warming has been reported to potentially have negative or positive impacts on crop production (Easterling et al. 2007, IPCC 2014, Rosenzweig et al. 2014, Asseng et al. 2015, Porter et al. 2017), depending on regions and crops. Wheat, as the third-largest crop, has attracted worldwide attention about how its productivity is impacted by climate change (Anderson 2010, Palosuo et al. 2011, Challinor et al. 2014). China is the largest wheat producer in the world, with 95% of wheat sowed in fall as winter wheat and the rest sowed in spring as spring wheat. Winter wheat requires a cool condition in the early growing stages to complete vernalization and trigger reproductive development (Zhao et al. 2016). As the increase of temperature in winter and spring are greater than in summer and autumn warming (Lobell 2007, Fan et al. 2015), this change would have a contrasting impact on winter and spring wheat yield in China. Understanding this impact is essential for the development of adaptation strategies to ensure food security in China and globally.

Warming impacts on wheat production have been studied through modelling (Li et al. 2010, Wang et al. 2012, Liu et al. 2014, 2016a, Martre et al. 2015, Asseng et al. 2015, 2017, Pirttioja et al. 2015, Rezaei et al. 2018), historical data analysis (Lobell et al. 2005, 2012, Lobell and Ortiz-Monasterio 2007, You et al. 2009, Tao and Zhang 2013, Tao et al. 2014), and artificial field experiments (Tian et al. 2012, Rich et al. 2015, Fan et al. 2015, Zhao et al. 2017, Zheng et al. 2017). Worldwide, the general consensus is that increase in temperature reduces wheat growth duration and grain yield if there are no adaptation strategies applied (Porter and Gawith 1999, Minoli et al. 2019), with 1 °C increase in global temperature reducing global wheat yield by 4.1%–6.4% depending on the methods used for yield projection (Liu et al. 2016b). In China, several crop models and empirical statistics studies indicated similar yield decline as a result of rising temperature, shortened growth duration, and increased risk of yield loss caused by extremely high temperature (You et al. 2009, Liu et al. 2016a). However, a few artificial...
warming studies found that warming could benefit wheat production in some places in China, where the mean growing season temperature is low and water supply is not limiting (Fang et al 2015, Zhao et al 2016). A systematic analysis of how warming impacts on yield of different wheat genotypes across climatic regions in China is clearly needed.

Here, we compiled data from field studies carried out at 12 locations in China, covering 14 cultivars, 27 site-years of the wheat yield in response to artificial warming to analyse the impact of temperature rise on wheat yield. These studies spread over the major growing regions of wheat in China (figure 1). In all experiments, winter wheat crops were grown with sufficient water and nutrient supply, and some spring wheat crops were with supplemental irrigation with diseases and pests properly controlled. The air temperature was increased by 1 °C–3 °C using infrared radiation lamps suspended above the ground in downwards-facing stainless-steel semi-circular mirror reflectors which enhanced the efficiency of radiation lamps (Fang et al 2015). Our objective is to depict a more complete picture of how different wheat genotypes respond to temperature rise across environments.

2. Methods

2.1. Datasets

A literature search was performed on field warming experiments of wheat in China through Web of Science, Google Scholar, and China National Knowledge Infrastructure (CNKI; www.cnki.net) with keywords wheat yield, artificial warming and China. We considered all peer-reviewed studies published before October 2017 in the major wheat growing region of China from which changes in wheat yield in response to artificial warming can be derived and quantified (table 1).

All field experiments deployed direct warming treatments for the whole growing season in field scales with infrared radiation lamps above the ground (Fang et al 2015). To focus on the impact of rising temperature on wheat yield, we only selected field experiments with sufficient nitrogen and water supply (i.e. without stresses). Twelve sites over the major wheat growing region in China were used in this study (figure 1), including nine sites with winter wheat and three sites with spring wheat. The cultivars used in the field experiments were all local representative cultivars. The wheat growing season temperate of those sites ranged from 9.2 °C to 16.1 °C (without warming, table 1). The field experiments used in this study included ambient control (CK, not warmed) treatment and artificial warming treatments, i.e. nighttime (NW), daytime (DW), or all-day warming (AW). Final observed wheat yield, yield components (spike number, grain number per spike, and 1000-grain weight), and wheat phenology (sowing, regreening, flowering and maturity dates) were all derived from the published studies. Site locations, wheat types, cultivars, treatment details, and references to the literature are given in figure 1 and table 1.

The county-level wheat grain yield was used to show the major growing region of wheat in China and helped to select the study sites. County-level data were obtained from the National Bureau of Statistics of China. Daily temperature data for all sites were obtained from the China Meteorological Administration, including maximum, minimum, and average temperature.

2.2. Change in wheat yield, yield components and phenology under warming treatments

To analyse wheat yield change in response to warming, percentage changes in yield and yield components are calculated as:

\[ \Delta Y\% = (Y_{\text{warm}} - Y_{\text{ck}})/Y_{\text{ck}} \]  

where \( Y_{\text{warm}} \) and \( Y_{\text{ck}} \) are the yield or yield components from the warming and ambient control treatment, respectively.

To analyse phenology change in response to field warming, the change is calculated as:

\[ \Delta P = P_{\text{warm}} - P_{\text{ck}} \]  

where \( P_{\text{warm}} \) and \( P_{\text{ck}} \) are the maturity date, pre- or post-flowering stage length from the warming and ambient control treatment respectively.

2.3. The response of wheat yield to the mean growing season temperature

To analyse the response of wheat yield to growing season temperature, linear mixed model (LMM) was used to derive the relationship between wheat yield and the mean growing season temperature. As cultivars have significant impacts on wheat yield, LMM was used to test if the association between wheat yield and growing season temperature exits after controlling for the variations in wheat cultivars. The mean growing season temperature was fitted as a fixed effect and wheat cultivar was fitted as a random effect, so the LMM was written as:

\[ \text{Yield} \sim T_m + (T_m|\text{Cultivar}) \]  

where \( T_m \) is the mean growing season temperature. The LMM was evaluated in R 3.5.1 using the algorithm implemented in the R package ‘lme4: linear mixed-effects models using Eigen and S4’ (https://github.com/lme4/lme4/). The significance of the fixed effect was tested using the likelihood ratio test with the \( R \) function drop1().

2.4. Extreme hot days calculation

In the previous study, Wang et al (2017) analysed the variations and uncertainties in the mathematic functions used to simulate temperature responses of
Table 1. Geographical location of the study sites, wheat cultivar, field warming treatments, and references of datasets.

| Region   | Site      | Latitude | Longitude | Cultivar                  | Year          | $T_m$ (°C) | Treatment | Irrigation | Reference                |
|----------|-----------|----------|-----------|---------------------------|---------------|------------|-----------|------------|--------------------------|
|          | Danyang   | 31.92    | 119.50    | Yangmai11*                | 2007–2008     | 11.02      | NW        | Sufficient | Zheng et al (2017)        |
|          | Dingxing  | 39.13    | 115.67    | Super-626*                | 2008–2011     | 9.17       | AW, NW    | Sufficient | Fang et al (2015)         |
|          | Lianyungang| 34.55    | 119.38    | Yannong19*                | 2009–2010     | 10.18      | AW        | Sufficient | Cao (2012)                |
|          | Nanjing   | 32.03    | 118.87    | Xumai31*                  | 2012–2013     | 11.03      | AW&DW&NW, NW | Sufficient | Tian et al (2012) Shi (2014) |
| Winter wheat | Nanjing | 32.03    | 118.87    | Yangmai13*                | 2012–2013 2013 | 11.03      | AW&DW&NW, NW | Sufficient | Tian et al (2012) Shi (2014) |
|          | Nanjing   | 32.03    | 118.87    | Yangmai11*                | 2012–2013 2013 | 11.03      | AW&DW&NW, NW | Sufficient | Tian et al (2012) Shi (2014) |
|          | Nanjing   | 32.03    | 118.87    | Yangmai11*                | 2012–2013 2013 | 11.03      | AW&DW&NW, NW | Sufficient | Tian et al (2012) Shi (2014) |
|          | Nanjing   | 32.03    | 118.87    | Yangmai11*                | 2012–2013 2013 | 11.03      | AW&DW&NW, NW | Sufficient | Tian et al (2012) Shi (2014) |
|          | Nanjing   | 32.03    | 118.87    | Yangmai11*                | 2012–2013 2013 | 11.03      | AW&DW&NW, NW | Sufficient | Tian et al (2012) Shi (2014) |
|          | Nanjing   | 32.03    | 118.87    | Yangmai11*                | 2012–2013 2013 | 11.03      | AW&DW&NW, NW | Sufficient | Tian et al (2012) Shi (2014) |
|          | Nanjing   | 32.03    | 118.87    | Yangmai11*                | 2012–2013 2013 | 11.03      | AW&DW&NW, NW | Sufficient | Tian et al (2012) Shi (2014) |

Winter wheat

Shanghai 31.21 121.13 Jiemai2* 2007–2008 10.83 AW Sufficient Ding et al (2013)
Shijiazhuang 38.07 114.35 Liangxin99* 2007–2009 9.41 NW Sufficient Zheng et al (2017)
Xuchang 34.83 116.67 Yumai7036* 2008–2010 10.17 NW Sufficient Zheng et al (2017)
Xuzhou 33.93 114.28 Yumai188* 2007–2010 10.73 NW Sufficient Zheng et al (2017)
Yucheng 36.83 116.57 NG1* 2010–2012 9.35 AW Sufficient Hou et al (2012)
Dingxi 35.58 104.62 Dingxi24* NG2** 2012 2011 16.13 AW AW NG +20% rainfall Zhang et al (2015) Wang (2013)
Spring wheat

Guyuan 36.03 106.47 Longchun15** 2001 14.29 AW +130 mm Xiao et al (2007)
Xidatan 38.86 106.36 Yongliang4* 2010 14.63 AW Sufficient Xiao et al (2011)

NG1 and NG2 indicate the cultivar names are not given in the articles. AW, NW and DW indicate all day warming, nighttime warming and daytime warming treatments, respectively. $T_m$ is the average temperature of the wheat growing seasons for the non-warming treatment. All the field experiments have at least three replicates, * and ** in the cultivar column indicates the warming increases/decrease the wheat yield significantly with $p < 0.05$ and $p < 0.01$, respectively, and indicates the warming has no significant impact on wheat yield.
physiological processes in 29 wheat models and then derived a set of new temperature response functions based on the newest knowledge and data. The new response functions reduced the error in wheat yield simulations across contrasting climatic regions when they were substituted in four wheat models. The optimum temperature for the rate of radiation use efficiency (RUE), pre- and post-flowing phenological development of wheat is 20 °C, 27.5 °C and 33 °C, respectively (Wang et al. 2017). Here we counted the days when the average daily temperature was over the optimum temperature for RUE, pre- and post-flowing phenological development, respectively. Besides, we counted the days with maximum temperature was over 32 °C (heatwave condition).

Then we compared the hot days in the warming treatment with the corresponding ambient control (CK, not warmed) treatment for each site-year to analyse the impact of extreme temperature caused by artificial warming. The T-statistic method was applied to test the significance.

3. Results

3.1. Warming impact on wheat yield varied with genotypes and environments

Pooling all data together revealed contrasting yield responses to warming for winter and spring wheat (figure 2(a)). For more than 90% of site-year-treatments, winter wheat yield increased while spring wheat yield declined with rising air temperature (black dots above zero and red triangles below zero). Only three site-year-treatments showed winter wheat yield decreased with rising temperature, i.e. all day warming treatment for cultivar Super-626 at Dingxing in 2008–2009 season, night warming treatment for cultivar Yangmai13 at Nanjing in 2012–2013 season, and AW treatment for one cultivar (name not given) at Yucheng in 2011–2012 season. In general, all the warming treatments, i.e. DW, NW, and AW, led to a yield increase for winter wheat.

The contrasting yield change is a consequence of the changes in yield components, i.e. 1000-grain weight, grain number per spike and spike number per meter squared (figures 2(b)–(d)). Averaged across site-years, grain number and 1000-grain weight increased by 4.1% and 4.2% respectively with each 1 °C warming for winter wheat but decreased by 18.0% and 11.0% (p < 0.05) for spring wheat. Spike number also increased with temperature for winter wheat but remained unchanged for spring wheat.

LMM results imply a significant positive relationship between grain yield and mean growing season temperature for winter wheat, but a negative one for spring wheat (figure 3). For winter wheat, the experiments covered a growing season temperature range of 7.5 °C–12.8 °C, grain yield increased with
Figure 2. Observed yield and yield components change in response to increasing temperature in the field warming experiments. Panels (a)–(d) represent the relative change in yield, spike number, grain number per spike, and 1000-grain weight of wheat, respectively, in response to increasing temperature. The black circles represent the changes of winter wheat and the red triangles represent the changes of spring wheat.

3.2. Warming impact on phenological development and length of the growing period
Warming led to 4 d and 12 d earlier maturity and shortened the whole growth duration for winter and spring wheat respectively (figure 4(a)). Counting the number of days with daily mean temperature above 0 °C as the active growing duration of wheat, i.e. days before and after overwinter (wheat will stop growth during overwinter duration when the temperature was less than 0 °C), the total duration of active growing duration was extended for winter wheat by an average of 11 d (5 d and 6 d for before and after overwinter, respectively), but shortened for spring wheat by 12 d across treatment (figure 4(a)). Warming accelerated pre-flowering phenological development similarly for winter and spring wheat, leading to shortened pre-flowering periods (from regreening to flowering) (figure 4(b)), while extended the post-flowering periods (from flowering to maturity) for winter wheat for most warming treatments (figure 4(c)). Each degree of warming advanced flowering time by approximately 10 d (p < 0.01). The post-flowering period was shortened with increasing temperature for spring wheat by 4.1 d °C\(^{-1}\) (p < 0.01). The whole growth seasons (from sowing to maturity) were shortened with increasing temperature for both winter and spring wheat (figure 4(d)). Averaged across all site-years, the warming treatment advanced the flowering and maturity dates 8.0 d and 6.9 d, respectively.

3.3. Extreme hot days and their potential impact
Field warming has little impact on days of average temperature over 20 °C (optimum temperature for RUE, figure 5(a)), 27.5 °C (optimum temperature for pre-flowering phenological development), and 33 °C

the temperature significantly \((R^2 = 0.17, p < 0.01)\), with a rate of 402.9 kg ha\(^{-1}\) °C\(^{-1}\). For spring wheat, yield declined with mean growing season temperature \((R^2 = 0.23, p < 0.1)\) at a rate of 607.1 kg ha\(^{-1}\) °C\(^{-1}\) in a temperature range of 13.8 °C–17.2 °C (figure 3).
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Figure 3. Observed yield change in response to the mean growing season temperature in the field warming experiments. LMM_slope represents the slope from the mixed linear model. The dash lines indicate the slope of the mixed linear model. The number and lines in black colour show the results of winter wheat and those in red colour show the results of spring wheat. The circles represent the changes of winter wheat and the triangles represent the changes of spring wheat. ∗∗∗ and ∗ indicate the significance level is 0.001 and 0.05 respectively.

Optimum temperature post-flowering phenological development (Wang et al. 2017). Days of average temperature over 27.5 °C and 33 °C are 0 for both field warming and normal conditions in this study. Field warming also has little impact on days of maximum temperature over 32 °C (figure 5(b)). In this case, it causes no significant heat stress increase for both wheat phenological development and biomass growth. Within the optimum temperature, warming increases both phenological development rate and biomass growth rate (figure 6). Generally, increasing phenological development rate shortens the duration of wheat growth and reduces final biomass and yield, while increasing of RUE increases the daily biomass accumulation and will lead to a positive effect. Thus, the interactions of these two stages on wheat grain yield in the warming are determined by the change rate of two physical processes in response to increasing temperature.

For the winter wheat in this study, the average growing season temperature ranged from 7.5 °C to 16.7 °C (red dash lines in figure 6). Within this regime, an increase in temperature accelerated the increase in RUE more rapidly than the phenological development processes, particularly for the post-flowering phenological development. However, within the temperature regime of the spring wheat (black dash lines in figure 6), the increase rate of RUE in response to warming slowed down and both the rates of pre- and post-flowering phenological development increased quickly. This might explain the different response of winter and spring wheat to warming in those field experiments in China.

4. Discussion

Our results contrast with the general perception that warming reduces wheat grain yield, which is the main conclusion of a majority of the previous studies based on crop modelling (Asseng et al. 2015, 2017), historical yield statistical data and climate recorders (Chavas et al. 2009, Xiao et al. 2013, Tao et al. 2014). Previous multi-model studies indicated that warming decreased wheat yield at a majority of wheat-growing locations when temperature increases imposed on the 1981–2010 period (Asseng et al. 2015, Pirttioja et al. 2015) and empirical studies of observed historical wheat yield also showed a decrease in wheat yield with warming (Tao et al. 2014, Xiao and Tao 2014). Our findings clearly showed that warming up +3 °C only reduced grain yield of spring wheat, but increased grain yield of winter wheat in most regions of China where wheat was sowed in autumn with reference temperature below 13 °C. This is also in contrast with the results of the most comprehensive modelling study of AgMIP-Wheat (Asseng et al. 2015, Pirttioja et al. 2015, Liu et al. 2016b, Wang et al. 2017), where a decline in both winter wheat and spring wheat yields with temperature rise was projected with an ensemble of ~30 wheat models for constant CO₂ levels in other regions.

These inconsistencies are likely attributable to differences in datasets and methods used for analysis and projections of wheat yield change in response to temperature rise. Most of the previous studies reported high-temperature limit wheat production used field experimental datasets in warmer regions with reference temperature above 13 °C.
Figure 4. Lengths of active growth durations (temperature >0 °C), pre- (days from regreening to flowering) and post-flowering periods (days from flowering to maturity) of wheat in response to increasing temperature. Panel (a) indicates changes in growth duration before winter, after winter, and overwinter for winter and spring wheat under ambient control (CK, not warmed) treatment and the warming treatment, respectively. Panels (b)–(d) indicate changes in the pre-flowering period, the post-flowering period, and the whole growing seasons (from sowing to maturity) under artificial warming treatment, respectively.

Figure 5. Changes in days with average temperature ($T_{\text{ave}}$) over 20 °C (a) and maximum temperature over 32 °C ($T_{\text{max}}$) (b) during the wheat growing season in response to warming. The average temperature of 20 °C is the optimal average temperature for wheat biomass growth (Wang et al. 2017). When maximum temperature is over 32 °C may cause heat stress for wheat.

(Ottman et al. 2012, Rosenzweig et al. 2014, Asseng et al. 2017). However, the impact of warming on wheat grown in environments below 12 °C was less considered and reported in China. Several previous studies have reported that the positive effect of temperature rise in some world regions has been regularly overlooked in recent discussions and studies on global warming effects on crop production (Pirttioja et al. 2015, Trnka et al. 2019). Pirttioja et al. (2015) explored the temperature and precipitation effects on both winter and spring wheat across a European transect with ensemble modelling approach and found the
optimum would be achieved with slight warming for winter wheat at Jokioinen, Finland.

Statistical analysis often relies on historical data covering multiple environments where management details and information on crop stresses (water, nutrient, pest, and disease) are unclear. Modelling results are usually subject to uncertainties in the process modules and limited datasets (cultivars and sites) used to validate the models used, leading to uncertainties in yield projections (Wang et al 2017). Our results summarized the data from individual warming experiments of wheat with reference temperature ranges from 7.5 °C to 17.2 °C under sufficient irrigation (except some spring wheat with supplemental irrigation) and fertilizer applications, thus most likely provide the yield changes of different wheat cultivars in response only to the temperature rise of 1 °C–3 °C. One limitation of those filed warming experiments is that almost only one representative wheat cultivar was planted at one site (except Nanjing and Dingxi). Cultivars would affect the response of wheat production to warming (Zheng et al 2017). To investigate the interactions of genotype and cultivar on wheat growth in response to warming, further field experiments with multiple cultivars across contrasting environments are needed.

Winter wheat accounts for 95% of wheat in China and its mean growing season temperature is below ~13 °C (You et al 2009). In most of the winter wheat growing season, the temperature is well below the optimum temperatures for phenological development, biomass growth, organ development and grain filling (Wang et al 2017). The derived yield changes of winter and spring wheat can be explained by the impact of temperature rise on the key developmental and growth processes of wheat. For winter wheat, warming only shortened the over-wintering period when the crop was dormant but extended both the pre- and post-winter growing durations, i.e. the active growing duration is considerably extended (11 d), but not shortened, which will benefit to winter wheat growth and yields. What’s more, for winter wheat, the prolonged pre-winter development promotes tillering and root development before winter, leading more large tillers, better water and nutrient use, and higher tiller survival, subsequently more spike numbers per plant (figure 2(b)). In addition, earlier spring growth under higher temperatures (figure 4(a)) benefit spikelet development resulting in large spikes (figure 2(b)) and extended post-flowering (figure 4(c)) leads to longer grain filling period and large grain size (figure 2(d)), as well as earlier mature avoided more hot days of maximum temperature over 32 °C for winter wheat (figure 4(a)). All these processes contribute to the yield increase. For spring wheat, however, most of these key phrases are shortened by temperature rise, leading to unchanged spike number (figure 2(b)), reduced grain number (figure 2(c)) and grain size

Figure 6. The relative rates of pre- and post- anthesis development, and radiation use efficiency (RUE) of wheat. The black and red dash lines show the mean growing temperature regimes of winter and spring wheat respectively in this study. The numbers in the brackets in the legends for the response lines indicate the minimum ($T_{min}$), optimum ($T_{opt}$) and maximum ($T_{max}$) temperatures with the unit of °C. The cardinal temperatures and the $f(T)$ function equation used to derive the curve are from Wang et al (2017). Reprinted by permission from Springer Nature Customer Service Centre GmbH; Macmillan Publishers Limited. Wang E, Martre P, Zhao Z et al 2017 The uncertainty of crop yield projections is reduced by improved temperature response functions Nat. Plants. Copyright © 2017.
According to a new report by the UN’s Intergovernmental Panel on Climate Change (IPCC), we probably to limit human-induced global warming to 1.5 °C (Myles et al. 2018). In this case, our results indicated that global warming likely has a positive impact on winter wheat yield in China. While temperature changes are the major factors in crop response to climate change, other factors like CO₂ concentration also play an important role in determining yields (Liu et al. 2016a). If considering the positive CO₂ impact, winter wheat yield may increase more in China. Even though global warming is expected to increase the frequency and intensity of severe water scarcity (SWS), which will negatively affect rain-fed wheat yield (Trnka et al. 2019), most of the winter yield in China is irrigated and the risk of an increased probability of SWS is quite low. In addition, it also needs to be noted that warming is generally conducive to more pets and disease epidemics (Tang et al. 2017), which might pose an even greater threat to wheat production.

In this study, we show that increasing temperature up to 3 °C increases winter wheat yield while decreases spring wheat yield in China through field warming experiments at multiple sites. Our results indicate that adaptation strategies for winter wheat production to climate change should focus on optimal water and nutrient management. Adaptation strategies like changing sowing dates and new cultivars with more heat tolerance can be suggested for spring wheat in China.

**Data availability statement**

The data that support the findings of this study are available upon reasonable request from the authors.

**Acknowledgments**

This work was supported by the Natural Science Foundation of China (Grant No. 42075193, 41375117 and 41905103), the National Key Research and Development Program of China (Grant No. 2019YFC1510205), and the Basic Research Funds–regular at the Chinese Academy of Meteorological Sciences (Grant Nos. 2019Z010 and 2018Y002).

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