



Extreme heat effects on perennial crops and strategies for sustaining future production



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ABSTRACT

Extreme heat events will challenge agricultural production and raise the risk of food insecurity. California is the largest agricultural producer in the United States, and climate change and extreme heat may significantly affect the state's food production. This paper provides a summary of the current literature on crop responses to extreme heat, with a focus on perennial agriculture in California. We highlight contemporary trends and future projections in heat extremes, and the range of plant responses to extreme heat exposure, noting the variability in plant tolerance and response across season, crop, and cultivar. We also review practices employed to mitigate heat damage and the capacity for those practices to serve as adaptation options in a warmer and drier future. Finally, we discuss current and future research directions aimed at increasing the adaptive capacity of perennial agriculture to the increased heat exposure anticipated with climate change. Collectively, the literature reviewed makes clear the need to understand crop responses and tolerances to heat within the context of climate change and climate extremes in order to sustain crop production, preserve agricultural communities, and bolster food security at local, national, and global scales.

1. Introduction

Extreme heat exposure can stress plants, stunt development, and cause plant mortality, which often results in reduced quality and lower yield in agricultural crops [1]. Diminished crop yields due to extreme heat can have cascading effects on global economies and heighten concerns around food availability [2–4]. Recent heatwaves in Europe [2,3], Russia [4], and the central United States [5] reduced yields for cereal crops, and in some instances led to significant commodity price increases and spikes in food insecurity. Warming anomalies have also caused significant losses in woody perennial cropping systems. For example, abnormally warm winter and spring temperatures in 2015 resulted in more than \$240 million in combined crop indemnity payments to almond, cherry, grape, pistachio, peach, and walnut growers in California [6,7]. These losses have widespread repercussions for California as the producer of more than two-thirds of US-grown fruits and nuts, including more than 99% of many US-grown high-value perennials [8].

California's Mediterranean climate – characterized by cold, wet

winters and warm, dry summers – coupled with elaborate infrastructure that enables widespread irrigation, makes the state ideal for cultivating a wide variety of crops. In such irrigated agriculture systems, where water application is the primary strategy employed to mitigate heat stress responses, increased heat exposure raises water demand and can strain limited water resources. During the mid-2010s California drought, surface water shortages and groundwater storage deficits limited water application as a heat management strategy [9]. Coupled with the dry, hot summer typical of a Mediterranean climate, the ongoing drought precipitated crop yield declines, fallowed lands, and an increased cost of water application [10]. During the height of the multi-year drought, the cost to the state's agricultural sector included direct losses in crop revenue of ~\$1.9 billion, total economic impacts topping \$5.5 billion, and job losses in the tens of thousands [10–12]. Although retail pricing for California crops only increased marginally due to a complex and globalized food system, the agricultural-sector job losses increased social, economic, and food insecurity for vulnerable communities across the state [13].

Highly seasonal precipitation regimes, as is the case in much of

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California, present a mismatch in water supply and plant-water demand resulting in reduced availability of water resources at the time it is most needed. Recent research suggests that most Mediterranean climates around the world will dry in the coming decades under climate change, though projections for California are more nuanced and include dramatic swings from exceptionally wet to exceptionally dry years [14–16]. Likewise, climate change is projected to increase average temperatures, heat extremes, and stress in these climates [17–19], and shift winter precipitation regimes from snow to rain, which may complicate water management and delivery [20]. In addition to these physical drivers, policy and regulation can reduce water availability through limiting access to surface or groundwater supplies. Current and future regulatory restrictions to groundwater pumping in California (e.g. [21,22]), anticipated warming, and asynchronous water availability relative to demand will undoubtedly challenge agricultural systems across the state.

One of the grand challenges facing society in the coming decades is to sustainably maintain – if not increase – agricultural production to meet the nutritional and caloric needs of a growing population. Given their importance in meeting global caloric needs, research relating climate change impacts on agriculture to food security often focuses on commodity crops (e.g. [23,24]). However, due to the economic importance of high-value specialty crops and the relationships between economic security and food security [25,26], understanding the myriad effects of climate change on perennial specialty crop production provides a unique framing for anticipating the broad and far-reaching impacts of climate change on food security. As the United States' leading agricultural state and one of the top 10 agricultural economies in the world [27], California is a fitting location to examine the effects of extreme heat exposure on perennial specialty crops and the adaptation strategies employed to ameliorate damages.

2. Methods

Here we provide a brief review of the current state of knowledge on the impacts of and adaptation strategies for detrimental heat exposure in California perennial specialty crops. We synthesize information from a variety of sources, including peer reviewed literature, state and national agricultural agency reports, and agricultural extension white papers. Our review focuses on those specialty crops with both high economic value as well as those identified by Kerr et al. [28] as having moderate or high sensitivity to summer temperature increases, and we further limit our review to select perennial crops: almonds, grapes, peaches, pistachios, and walnuts. While these crops may be grown widely across the state, we primarily restrict our geographic references to 6 agricultural regions within California, chosen and delineated based on crop density, climatic considerations, and groundwater basin boundaries (Fig. 1); however, we do not limit our literature review to only studies conducted in these regions. Similarly, because what constitutes extreme temperatures can vary depending on the crop species, cultivar, and phenological phase, we do not limit our literature review to an *a priori* definition of 'extreme.'

The review is organized as follows: We first provide a brief review of current trends and future projections of heat extremes across California. We then present an overview of each of our selected crops within the context of California agriculture, and examine the effects of cool- and warm-season heat extremes on crop development, yield, and quality. Finally, we explore available adaptive management strategies for California perennial specialty crops, and identify areas of on-going heat-related research in these cropping systems.

3. Defining heat extremes

Heat extremes are often considered warm season hazards, but anomalously warm temperatures during the cool season can also affect agricultural and natural systems. In California, both cool- and warm-

season heat events are principally driven by global- and synoptic-scale atmospheric patterns [19,29–31], though local-scale wind patterns can also lead to late-season heatwaves in southern California [19]. Regardless of season of occurrence or atmospheric driving mechanism, there is no consistent means of quantifying temperature extremes. Definitions or characterizations of extremes may incorporate fixed threshold values, occurrence probabilities or percentile values, temporal variations, diurnal considerations, or degree of impact on ecosystems and society [19,32,33]. Despite variable definitions for heat events, numerous studies have attributed trends in the intensity, frequency, and duration of heat extremes to anthropogenic climate change [34].

Across California, contemporary average annual temperatures rose $\sim 1.1^\circ\text{C}$ relative to the first half of the 20th century, and are projected to increase by $\sim 3.1\text{--}4.9^\circ\text{C}$ by 2100 [20]. Cool-season temperatures have also increased and anomalous heat events during the cool season have become more frequent over the past ~ 35 years [30]. Climate change projections suggest a continued warming trend in cool-season temperatures, with minimum temperatures warming faster than cool-season average temperatures [35,36]. Trends in summer heat wave intensity and frequency in California have also been positive over the long-term observed period and climate change is projected to further these trends [19,37]. However, the magnitude of projected changes in heat extremes varies across the state and the proportionate intensity of heat waves in some regions may be moderated by background warming [19].

To illustrate the spatial heterogeneity in projected changes, we calculated the anticipated differences in three measures of extreme heat exposure across California for the warm (April–September) and cool (October–March) seasons using observed [38] and projected [39] daily climate data. For each season, we compared contemporary (1981–2010) and end-of-century (2070–2099) climatologies for the average number of days with $T_{\text{max}} > 38^\circ\text{C}$ (Fig. 2a, d), the average number of days with $T_{\text{max}} > 98^{\text{th}}$ percentile of contemporary T_{max} ($> T_{\text{max},98}$, Fig. 2b, e), and the average number of 3-day $T_{\text{max},98}$ heat-waves (Fig. 2c, f). We encourage the reader to refer to these projected changes in extreme heat in light of the following sections, which review crop-specific heat responses and the associated adaptive measures.

4. Crop response to extreme heat

4.1. California perennial agriculture

California is the primary or sole producer of US-grown almonds, grapes, peaches, pistachios, and walnuts (Table 1). Collectively, these high-value perennials cover ~ 2.45 million acres and generate more than \$14 billion in cash receipts, comprising more than 28% of the state's direct agricultural value [8]. With the exception of winegrapes, which have significant acreage in coastal regions, the majority of these crops are grown in California's Central Valley (comprised of the Sacramento and San Joaquin Valleys, and the Sacramento-San Joaquin Delta region), with additional acreage in the Salinas, Coachella, and Imperial Valleys (Fig. 1). Although management practices, cultivar selection, and – for some crops – life history traits make these perennials well-adapted to California's climate, projected increases in the frequency, intensity, and duration of extreme heat will likely impact cultivation.

4.2. Crop responses to cool-season heat exposure

For crops well-adapted to summer heat, detrimental heat exposure occurs primarily during the cool season, when anomalously warm temperatures occur during dormancy and/or bloom. Many temperate-climate perennials require the accumulation of chill for dormancy release and flowering and fruit development, with the amount of necessary exposure to cool temperatures ranging from fewer than 200 to

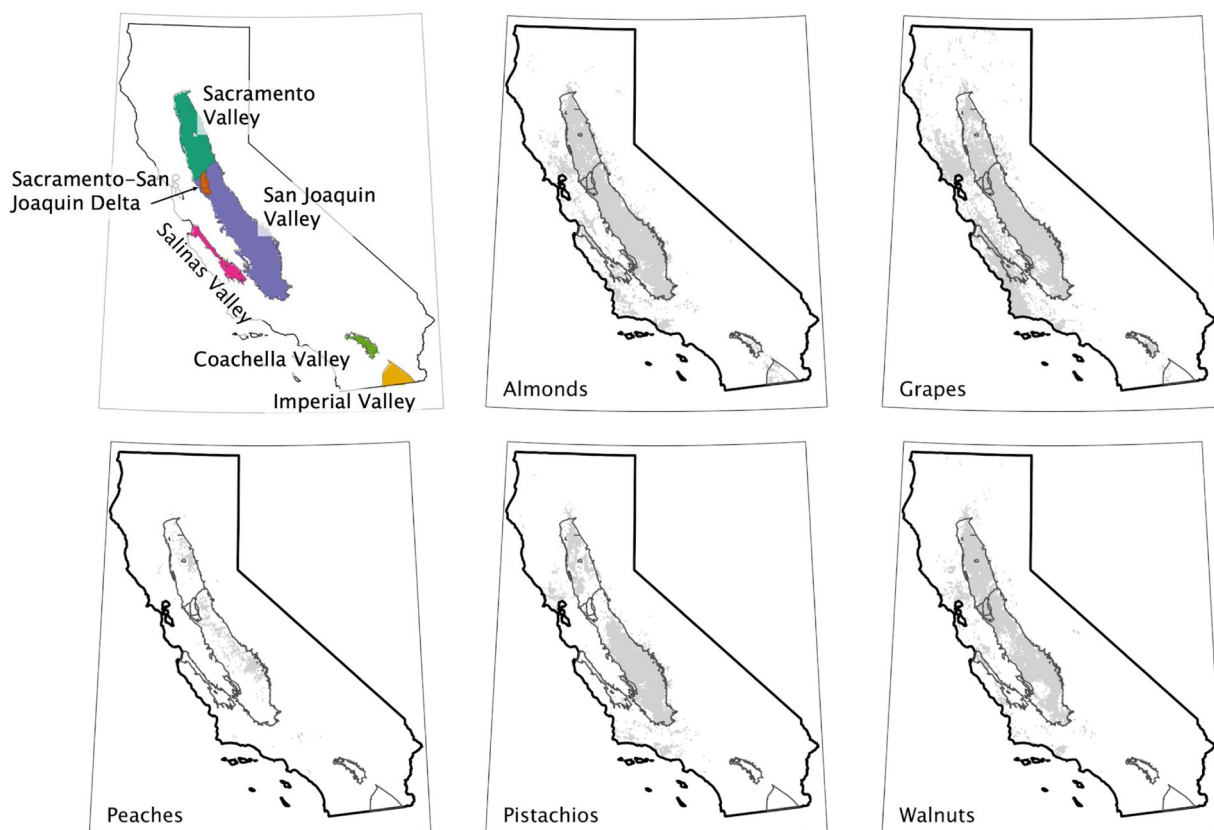


Fig. 1. Almonds, grapes, peaches, pistachios, and walnuts are largely concentrated within 6 California agricultural regions, with the majority of cultivation falling within the Sacramento and San Joaquin Valleys and Delta, which collectively comprise California's Central Valley. Grapes are a notable exception, with significant cultivation of winegrapes occurring in coastal hills south and west of the Salinas Valley, and west of the Sacramento Valley.

more than 1000 chill hours (i.e. hours below 7.2°C), depending on the crop and cultivar (Table 2). Exposure to anomalous warmth during dormancy can delay or prevent chill accumulation, which can cause delayed or asynchronous bloom, a compressed flowering and pollination window, delayed vegetative development and altered leaf morphology, fruit set failure, and reduced yields [40–42]. The 2015 California pistachio crop was devastated by a warm winter and subsequent insufficient chill, which resulted in more than \$180 million in losses [6,7].

Crop insurance claims citing heat exposure as the cause of indemnity identify the spring flowering and fruit set period as a heat-sensitive period for almonds, pistachio, and peach (Fig. 3; [7]). In almonds, extreme or unseasonably warm temperatures during bloom can desiccate and reduce receptivity of stigmas, shorten the effective pollination period, and subsequently limit fruit set (e.g. [43]), while in peaches, high early-spring temperatures have been linked to a decrease in the size of fruit at harvest [44]. Additionally, research suggests that temperatures above ~30°C during flowering can be detrimental to the hormone production needed for cell division and differentiation in almond [45] – a relationship that may hold true for other *Prunus* species like peach. Further, though insurance data suggest cool-season heat exposure in grapevine is less problematic than during other times of year, extreme heat during bloom in grapes can result in shortened floral length and early flower drop, reduced pollen viability, limited fruit set, and fewer berries per cluster [46,47].

4.3. Crop responses to warm-season heat exposure

There is limited literature on the effects of warm-season heat extremes on perennial crops in California, likely because detrimental impacts have only recently been frequent enough to prompt directed

response from the research community. Current understanding in the state – where irrigation provides a buffer for heat stress – suggests that the negative effects of warm-season extreme heat on perennial crops are largely a function of water stress. During water stress, stomata close to prevent water loss, but this comes at the cost of reduced carbon capture and higher leaf temperatures. Once stomata close, leaf water loss is then limited to a residual amount through the cuticle or leaky stomata. Cuticular conductance is known to increase exponentially above a phase transition temperature [48], and because of the high vapor pressure deficit associated with high air temperature, Cochard [49] recently proposed that leaf residual transpiration increases sharply under hot conditions, which could lead to catastrophic failure in the plant hydraulic system. Further work is needed to test this hypothesis across a greater diversity of species and in irrigated agricultural systems.

The combination of heat and water stress has great potential to affect crop yield, size, and quality. For example, moderate-to-severe water stress during nut development can reduce yield, size, and quality in almond and pistachio (e.g. [50,51]). Similarly, modeled effects of water stress in peach show reductions in fruit size, though moderate water stress may simultaneously increase fruit quality as sugar concentrations increase due to lower fruit water content [52]. In grapevine, though heat tolerance and physiological response varies across cultivars and genotypes [53], research has shown that temperatures > 35°C may slow physiological processes and can scar, crack, or discolor berries, irrespective of water application [47]. Extreme heat can also decrease winegrape berry size and fresh weight, particularly when exposure occurs during veraison and mid-ripening [46]. Further, extreme heat exposure during ripening can influence sugar accumulation, phenolic development, total phenol and anthocyanin concentrations, soluble solids, and proline and malate concentrations [54] – all of which can

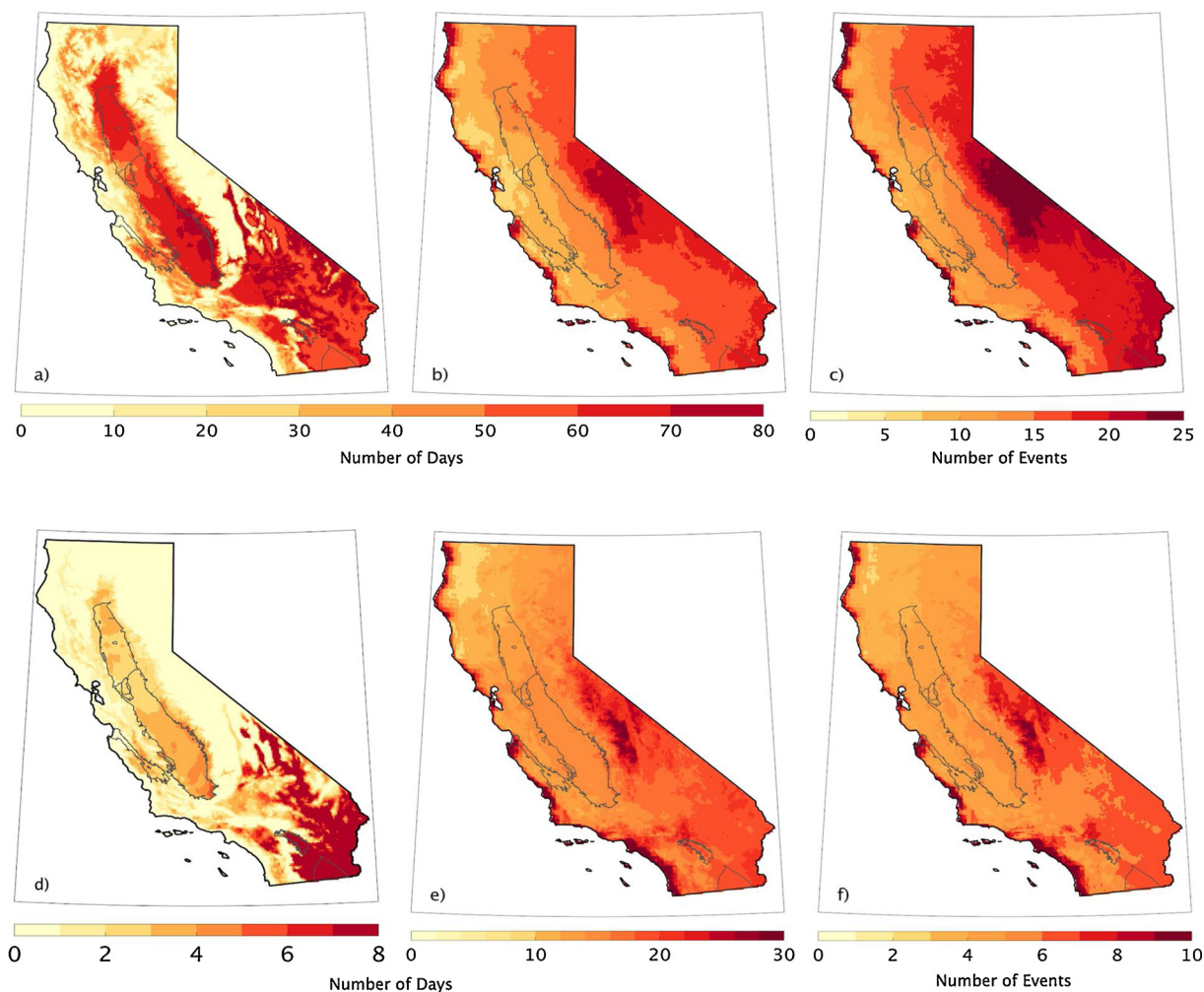


Fig. 2. The projected change between the observed contemporary (1981–2010) and modeled future (2070–2099, RCP 8.5) average annual number of (a) warm-season days with $T_{max} > 38^{\circ}C$, (b) warm-season days with $T_{max} > 98$ th percentile of observed 1981–2010 annual daily T_{max} , (c) warm-season 3-day heatwave events with $T_{max} > 98$ th percentile of observed 1981–2010 annual daily T_{max} (d) cool-season days with $T_{max} > 38^{\circ}C$, (e) cool-season days with $T_{max} > 98$ th percentile of observed 1981–2010 annual daily T_{max} , and (f) cool-season 3-day heatwave events with $T_{max} > 98$ th percentile of observed 1981–2010 annual daily T_{max} , Where the warm (cool) season is defined as April–September (October–March).

Table 1

The total California acreage and crop cash receipts for 5 selected high-value perennial crops, as well as the national (CDFA, [8]) and global (FAO [95],) rank in crop production. Data are from 2017.

Crop	Area (x 1000 acres)	Value (x \$1,000,000)	National (Global) Rank
Almond	1000.0	5,603.9	1 (1)
Grapes (all)	829.0	5,793.2	1 (3)
Peaches	38.3	371.5	1 (5*)
Pistachios	250.0	1,014.5	1 (2)
Walnuts	335.0	1,593.9	1 (2)

* Global production values include nectarines.

shape the winemaking process and ultimately wine quality characteristics such as color and aroma (e.g. [55]).

4.4. Projected future climate effects on heat exposure

As climate change increases average and extreme maximum cool-season temperatures, the reduction in chill accumulation across much of California (Fig. 4) may reduce areas with suitable chill for some of the state’s high-value perennials. For example, for cultivars requiring > 700 chill hours, ~ 50 –75% of California’s Central Valley may

not receive reliably sufficient chill for peach cultivation by mid-century, and as little as 2–10 % of the region may remain suitable by the end of the 21st century [56]. Similarly, the high chill requirements of pistachios and walnuts may eliminate their cultivation in California as early as 2060 (Table 2; Fig. 4; [56]). Further, as slowed chill accumulation can delay bloom in perennials, climate change may shift this sensitive development period into the warmer weeks of spring, increasing the risk of extreme heat exposure during flowering. However, warmer spring temperatures can also accelerate floral development (e.g. [57,58]), which may compensate for any delays in bloom and allay heat-induced damages that would otherwise result from later flowering.

Average and extreme maximum temperatures during the warm season are also projected to increase under future climate scenarios [20]. These warming scenarios will have mixed effects on perennial crop yields across the state [59], and may lead to shifts in the geographic distribution of crops such as winegrapes [60]. Specifically, increased frequency of extreme heat days ($> 35^{\circ}C$) over the 21st century may reduce suitability for winegrape production across much of California’s Central and North Coasts and Salinas Valley [61]. However, these future distribution and suitability models are not based on grapevine physiology [62], and adaptive practices were not considered despite adaptive management having the capacity to cut potential California winegrape production losses by more than half [63].

Table 2

Approximate range of chill requirements for selected high-value perennial crops. Minimum chill requirements vary across cultivars. Cultivars highlighted here (provided in italics) are examples of California’s commonly-grown cultivars.

Crop	Approximate Chill Hours (< 7.2°C)	Source
Almond	200–600	
	<i>Nonpareil</i>	400 [96]
Grape	100–400	
	<i>Chardonnay</i>	135 [97]
	<i>Cabernet Sauvignon</i>	395 [97]
Peach	400–1000	
	<i>O’Henry</i>	750 [98]
Pistachio	700–1000	
	<i>Kerman</i>	700 [99]
	<i>Peters</i>	900 [99]
Walnut	400–1500	
	<i>Hartley</i>	1000 [100]

5. Adaptive measures and current research for managing extreme heat exposure

5.1. Irrigation

Current practices for ameliorating warm-season heat events are largely limited to altering the amount and timing of irrigation water application. While irrigating to meet the full evaporative demands of crops may be ideal for reducing plant stress during extreme heat, mild water stress controlled through deficit irrigation strategies may provide improved crop quality. For example, regulated deficit irrigation (RDI) during early- and mid-summer hull split in almonds can result in more uniform maturity and reduce the damaging effects of hull rot [64], and RDI in peach production can provide water savings while improving crop quality [65]. In winegrapes, carefully-managed water stress can reduce water use and control vegetative vigor while maintaining yield and quality in [66].

Future climate conditions are likely to challenge the reliance on irrigation as a management strategy for extreme heat exposure. For example, increased groundwater withdrawals — particularly during

hot-drought events — will likely result in the application of water with suboptimal quality (e.g., greater salinity) [67]. With the widespread adoption of high-efficiency irrigation systems, quickly applying large amounts of water to may be difficult, and if extreme heat occurs during critical development stages that do not tolerate water stress (e.g. late-summer bud differentiation in almond, or prior to veraison in grapevine), there may be greater limitations to alternative irrigation scheduling. Conversely, saturating soils may incite other production challenges, such as increased disease susceptibility [68].

Recent research efforts have focused on improving irrigation efficiencies, assessing rootstock tolerance to limited water application, and the widening use of *in situ* measures of soil water availability and plant water stress to improve irrigation scheduling [69,70]. Additionally, new remote sensing evapotranspiration toolkits based on thermal imagery will improve winegrape growers’ ability to quantify additional water needs during heatwaves [71], and peach growers may increase water savings through adopting irrigation recommendations derived through real-time thermal infrared temperature data [72].

5.2. Site management

Several additional management strategies have the capacity to mitigate damage due to extreme heat. Cover crops can act to improve soil health through high organic matter and microbial biomass, and reduce summer orchard temperature [73,74], offering an adaptive management strategy for locations and crop systems most concerned with warm-season heat exposure. However, we note that the benefits of cover crops can vary by cover type (e.g. legumes vs. grasses), and in spring, cover crops have been shown to reduce the amount of available soil water and increase frost risk [74,75]. Shade nets may help to mitigate impacts of warm-season heat extremes and may improve fruit quality in peaches [76,77], though shading in grapes, while cooling the canopy, has in some cases been shown to have detrimental effects on anthocyanin and phenolic development in berries, which are important to grape quality [78,79]. In grapevine, planting new vineyards with a northeast-southwest orientation and altering trellis style to provide greater shade may be preferred as these approaches can reduce incoming solar radiation exposure and mitigate sun- and heat-induced

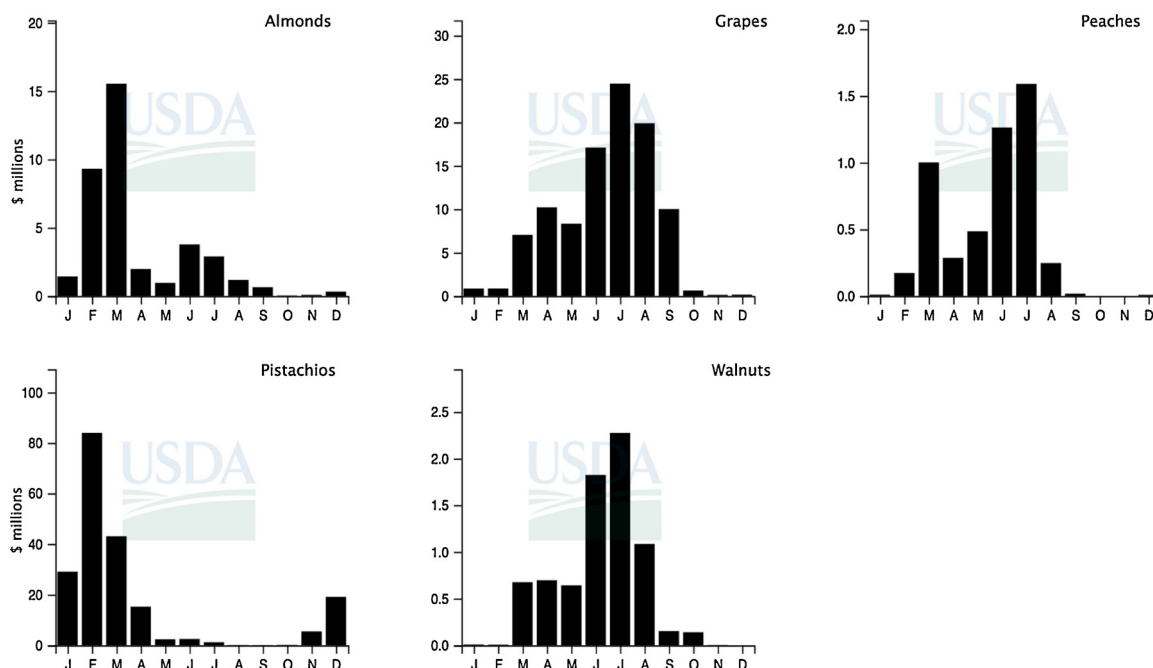


Fig. 3. Total crop losses (y-axis) by month (x-axis) over the 1989–2017 period, where the cause of loss was listed as “Heat.” Losses are represented by insurance indemnity payments in millions of dollars. Graphs downloaded from AgRisk Viewer [7].

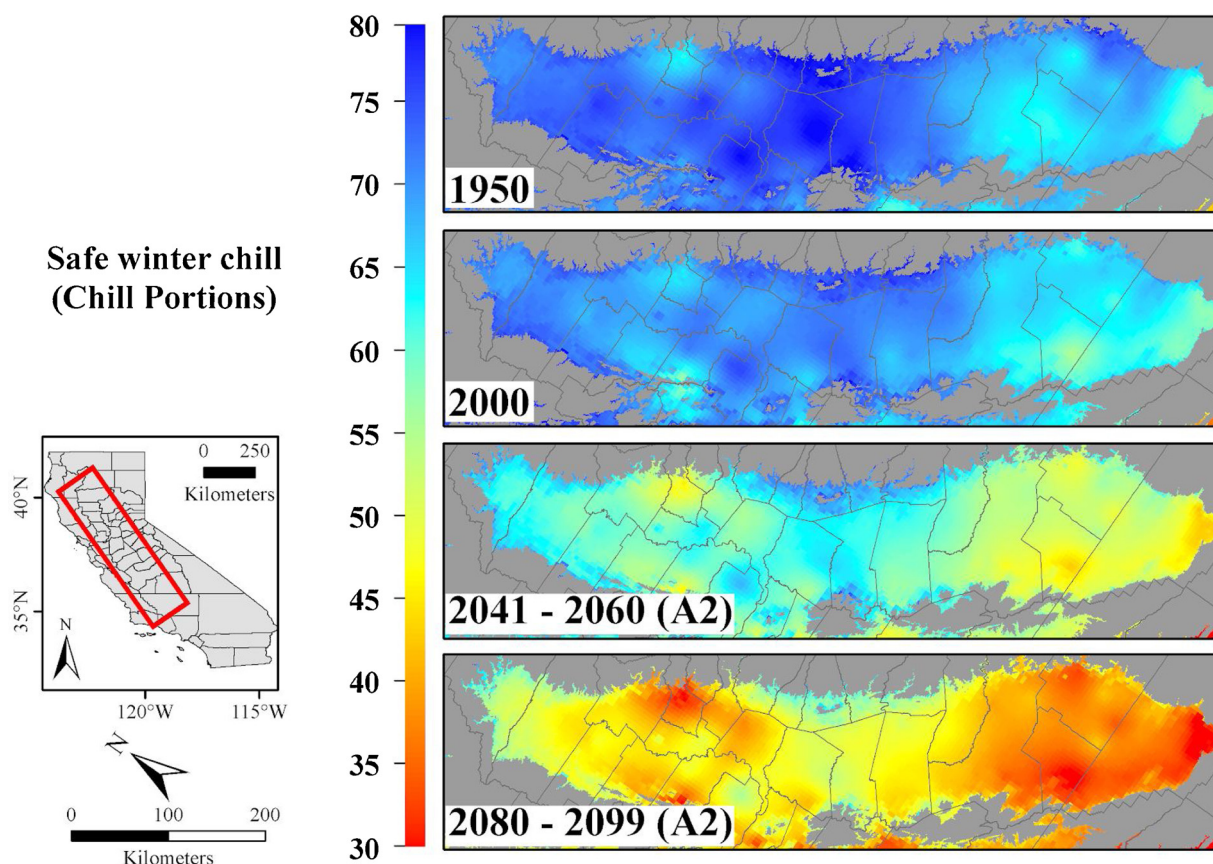


Fig. 4. Changes in the 10th quantile of winter chill accumulation over the Central Valley of California under modeled historic and future climate scenarios [56].

damages [80].

Research on future site suitability and bioclimatic niche have identified the potential need and geographic options for the translocation of some crops, such as winegrapes and almonds, to higher latitudes, altitudes, or more coastal regions where cooler climates mitigate increases in average and extreme warm temperatures [58,60,61]. However, while shifting crop geographies may provide a potential long-term adaptive strategy, this option requires appreciable capital and would likely be met with challenges such as competing land use; water availability; additional costs associated with crop processing, distribution, and industry marketing; and sociological considerations such as regional culture.

5.3. Cultivar selection

In crops with a wide range of chill requirements, selecting for cultivars with lower chill needs can provide some adaptive capacity to warming winters, and in some crops, response to insufficient chill accumulation may be influenced by rootstock [81,82]. Cultivar and rootstock selection can also provide some resiliency to warm-season heat extremes when selecting for heat and/or drought tolerance in pistachio [83] and grapevine [53,84,85].

Current drought-related research in rootstock includes efforts to identify salt-tolerant rootstocks [86], while in crop breeding programs, heat tolerance studies involve the development of low-chill varieties for cultivation in subtropical climates (e.g. peaches [87]). Researchers have noted the importance of collecting, cataloguing, and using existing genetic diversity – often from crop wild relatives – for future food security [88,89]. Research has also identified heat tolerance as being highly complex, plastic, likely polygenic, and variable across species, variety, and developmental stage, making successful breeding for heat tolerance time consuming and costly [90]. However, biotechnology

improvements may provide future opportunities to develop heat-tolerant crops in a timely and cost effective manner by capitalizing on genetic resources such as USDA Agricultural Research Service germplasm repositories [91,92].

6. Concluding remarks

In this review we highlight how more frequent, intense, and longer-duration heat extremes projected under climate change, especially in combination with background warming, may influence and/or stress perennial crops, and potentially limit crop production and reduce crop quality. We underscore that the sensitivity of perennial crops and their vulnerability to heat-induced damage can vary widely by crop, cultivar, and development phase. Additionally, we present adaptive strategies to mitigate damages from extreme heat exposure, though we note that successful adaptation depends on the availability of technological or biological solutions, as well as policy and economics [93]. However, even when accounting for adaptive action, climate change is nonetheless anticipated to have wide-ranging impacts on agricultural production across California, the US, and around the world [59,94].

While we have discussed what is known about the effects of, and adaptation measures for, extreme heat on perennial crops, we also elucidate that there are numerous gaps in knowledge surrounding crop tolerance and response to extreme heat, appropriate adaptive strategies, and what the intersection of these responses and strategies may mean for crop production broadly. The impacts of heat stress on agricultural systems are not a suppositional problem; rather, they are being experienced across California and around the globe in the present, and their wide-ranging effects emphasize the exigency for focused research on crop responses and sustainable adaptation strategies. Ultimately, both fundamental and applied research will be critical if we are to meet the challenges of preserving crop production, bolstering agricultural

communities and the agricultural economy, and strengthening food security at local, national, and global scales in the face of climate change and associated heat extremes.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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