中国生态农业学报(中英文) 2024 年 11 月 第 32 卷 第 11 期
Chinese Journal of Eco-Agriculture, Nov. 2024, 32(11): 1891−1902

DOI: 10.12357/cjea.20240114

CSTR: 32371.14.cjea.20240114

钟苑宁, 王慧丽, 高碧玮, 乔匀周, 马玉诏, 李永鹏, 董宝娣. 玉米高温胁迫研究热点及前沿探究[J]. 中国生态农业学报(中英文), 2024, 32(11): 1891−1902

ZHONG Y N, WANG H L, GAO B W, QIAO Y Z, MA Y Z, LI Y P, DONG B D. Research hotspots and frontiers of heat stress in maize[J]. Chinese Journal of Eco-Agriculture, 2024, 32(11): 1891−1902

玉米高温胁迫研究热点及前沿探究*

钟苑宁[1,2], 王慧丽[1], 高碧玮[1], 乔匀周[1], 马玉诏[1], 李永鹏[1], 董宝娣[1,2**]

(1. 中国科学院遗传与发育生物学研究所农业资源研究中心/中国科学院农业水资源重点实验室/河北省节水农业重点实验室 石家庄 050022; 2. 中国科学院大学 北京 100049)

摘 要: 玉米作为全球第一大粮食作物, 在维护全球粮食安全方面具有至关重要的地位。然而, 全球气候变暖导致高温天气频发, 对玉米的生长和产量造成了严重限制。因此, 深入探究全球玉米高温胁迫领域的研究热点和前沿趋势, 有助于应对气候变化带来的高温挑战, 促进玉米产业的可持续发展。本文利用 CiteSpace 软件, 对 1990—2023 年间 Web of Science 核心数据库收录的 4255 篇玉米高温胁迫的相关论文进行关键词共现、聚类和突现分析。结果表明, 玉米高温胁迫领域的研究热点主要集中在 4 个方面: 玉米在高温胁迫下的生长与产量变化、生理响应、分子机制和应对策略。深入探索这 4 个方面的研究进展, 发现不同生育期的高温胁迫对玉米生长发育和产量形成构成不同程度的伤害, 各生育期高温胁迫引发的产量损失减产幅度由高到低表现为花期>灌浆期>穗期>苗期; 高温胁迫还会引起玉米多个生理生化特征的变化, 包括光合作用受损、生物膜透性增加、活性氧过度积累和激素失衡等; 玉米响应高温胁迫的分子机制研究, 重点关注基因表达和热休克蛋白运作, 但耐热机制仍未明晰; 通过综合运用农艺措施与育种技术, 包括播期调整、科学水肥管理和生长调节剂的合理施用以及耐热品种的培育, 可以有效缓解高温胁迫, 促进玉米高产稳产。此外, 玉米响应高温胁迫的转录调控机制是该领域的关键研究前沿, 也将是未来较长时间内研究的热门课题。本文全面回顾了过去 34 年玉米高温胁迫领域的文献, 为玉米耐高温研究及缓解措施的制定提供了有益参考。

关键词: 玉米; 高温胁迫; CiteSpace; 生长响应; 分子机制; 应对策略; 转录调控

中图分类号: S513

Research hotspots and frontiers of heat stress in maize*

ZHONG Yuanning[1,2], WANG Huili[1], GAO Biwei[1], QIAO Yunzhou[1], MA Yuzhao[1], LI Yongpeng[1], DONG Baodi[1,2**]

(1. Center for Agricultural Resources Research, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences / Key Laboratory of Agricultural Water Resources, Chinese Academy of Sciences / Hebei Key Laboratory of Agricultural Water-Saving, Shijiazhuang 050022, China; 2. University of Chinese Academy of Sciences, Beijing 100049, China)

Abstract: Maize is the largest food crop in the world, and it plays a vital role in maintaining global food security. However, global warming, which has led to frequent high-temperature weather events, has severely limited the growth and yield of maize. Therefore,

* 国家重点研发计划项目 (2021YFD1901003-01) 和河北省自然科学基金项目 (C2021503006) 资助

** 通信作者: 董宝娣, 主要研究方向为作物绿色高效用水。E-mail: dongbaodi@126.com

钟苑宁, 主要研究方向为作物逆境生理。E-mail: zhongyuanning21@mails.ucas.ac.cn

收稿日期: 2024-03-07 接受日期: 2024-05-21

* This study was supported by the National Key Research and Development Project of China (2021YFD1901003-01) and the Natural Science Foundation of Hebei Province (C2021503006).

** Corresponding author, E-mail: dongbaodi@126.com

Received Mar. 7, 2024; accepted May 21, 2024

an in-depth exploration of research hotspots and frontiers in the field of high-temperature stress in maize worldwide will help to cope with the challenges brought about by climate change and promote the sustainable development of maize industry. In this study, CiteSpace software was used to analyze the keyword co-occurrence, clustering, and brust of 4255 papers related to high-temperature stress in maize included in the Web of Science core database from 1990 to 2023. The results showed that the research hotspots mainly focused on four aspects: growth and yield changes, physiological responses, molecular mechanisms, and coping strategies of maize under high-temperature stress. Through an in-depth exploration of the research progress in these four aspects, it was found that high-temperature stress at different growth stages caused different degrees of damage to maize growth and yield formation, and the yield loss caused by high-temperature stress at each growth stage ranged from high to low as follows: flowering stage > filling stage > heading stage > seedling stage. High-temperature stress caused changes in multiple physiological and biochemical characteristics of maize, such as impaired photosynthesis, increased biofilm permeability, excessive accumulation of reactive oxygen species, and hormonal imbalance. The molecular mechanism of maize in response to high-temperature stress was mainly on gene expression and heat shock protein operation, but the specific heat tolerance mechanism is still unclear. Through the comprehensive application of agronomic measures and breeding techniques, such as sowing date adjustment, scientific water and fertilizer management, rational application of growth regulators, and cultivation of heat-tolerant varieties, high-temperature stress can be effectively alleviated and a high and stable yield of maize can be obtained. In addition, the transcriptional regulation mechanism of maize in response to high-temperature stress is a current research frontier and will be an important topic for future research. This study comprehensively reviewed the literatures on high-temperature stress in maize in the past 34 years and provides a useful reference for the study of high-temperature resistance of maize and formulation of mitigation measures.

Keywords: Maize; Heat stress; CiteSpace; Growth response; Molecular mechanism; Coping strategies; Transcription regulation

气候变暖对全球农业生产和粮食安全构成巨大威胁。与 1951—1980 年相比, 过去 10 年 (2014—2023 年) 的全球平均气温上升了 0.93℃[1-2]。预计到 2040 年, 全球升温幅度将突破《巴黎协定》设定的 1.5℃ 的温控目标[3]。气温升高会造成农作物产量显著下降: 全球平均气温每升高 1℃, 主粮作物将减产 19.7% [玉米 (*Zea mays*): 7.4%; 小麦 (*Triticum aestivum*): 6.0%; 水稻 (*Oryza sativa*): 3.2%; 大豆 (*Glycine max*): 3.1%][4]。同时, 随着全球人口的持续增长, 粮食需求也随之增长。预计到 2050 年, 全球粮食必须增产 70% 才能满足新增人口需求[5]。

玉米是重要的粮食、饲料和工业原料作物, 具有较高的产量潜力和经济效益, 在全球粮食安全保障方面都发挥着至关重要的作用[6-9]。玉米是全球产量最高的粮食作物, 其总产量已超过 10 亿 t[7], 为全球人口提供了 19.5% 的热量[8]。玉米也是我国第一大粮食作物, 2023 年其种植面积和总产量分别占全国粮食作物的 37.2% 和 41.5%[9]。然而, 玉米在生育期内常常遭受频繁且严重的高温胁迫, 表现为光合速率降低、蒸腾速率增加、花粉活力下降、细胞衰老加速、灌浆时间缩短等, 穗粒数和粒重降低, 最终对产量造成严重的负面影响[10-15]。在气候变暖背景下, 高温胁迫已成为玉米生产面临的严峻问题。

针对高温胁迫这一突出问题, 众多国家的学者们开展了广泛而深入的研究, 并积累了丰富的研究论文。文献计量法作为一种新兴策略, 能够从海量的文献中高效、准确地挖掘出有价值的信息, 进而对某一领域的研究现状和发展趋势进行数学评估[16]。然而, 尚未有学者利用文献计量法对玉米高温胁迫领域的研究成果进行系统性探索。因此, 本文基于 Web of Science 数据库, 运用 CiteSpace 软件, 对 1990—2023 年期间发表的全球玉米高温胁迫领域的论文进行可视化分析。通过关键词共现、聚类与突现等方法, 结合对文献的细致研读, 系统梳理该领域的研究热点和前沿, 旨在为进一步推动该领域的发展提供理论依据。

1 文献来源与研究方法

1.1 文献来源

本文使用的文献源自 Web of Science 核心合集数据库的“Science Citation Index Expanded (SCI-EXPANDED)--1900-present”子库。文献检索策略设置为: 主题=(maize OR corn OR zea mays) 和主题=(heat stress OR high temperature stress OR thermal stress), 时间范围为 1990—2023 年, 最终搜集到 4255 篇玉米高温胁迫领域的相关文献。

1.2 研究方法

采用 CiteSpace 6.2.R4 高级版软件, 对所选文献进行可视化分析。CiteSpace 功能区的参数设定如下: 时间范围为 1990 年 1 月至 2023 年 12 月, 时间切片长度为 1 年; 节点类型选择关键词, 节点关联强度采用 Cosine 算法, 节点筛选方式使用 g-index 标准, k=5; 图谱网络裁剪方式选择寻径网络法 (pathfinder)、精简切片网络 (pruning sliced networks) 以及合并网

络 (pruning merged network); 其余参数保持默认。基于上述操作, 利用搜集到的文献进行关键词共现、聚类及突现分析, 旨在揭示玉米高温胁迫领域的研究核心、热点及前沿。

2　研究核心

出现频次高且中介中心性强的关键词, 通常被视为某一领域的核心主题[17-18]。为深入了解玉米高温胁迫领域的研究焦点, 统计了排名前 15 的高频关键词的频次及其中心性 (表 1)。结果显示“Yield”“Growth”“Tolerance”和“Gene expression”等高频关键词具有较高的中心性, 这说明过去 34 年的研究主要聚焦于产量、生长表现、耐热性和基因表达等方面。

3　研究热点

3.1　关键词聚类

玉米高温胁迫研究的关键词聚类结果包括 15 个聚类 (表 2), 该聚类的质量评价指标 Q=0.8169>0.3, S=0.9361>0.7, 说明聚类结构显著, 结果可信[19]。根据主要关键词, 将紧密相关且相似的聚类整合, 最终凝练出玉米高温胁迫领域热度最高的 4 个主题: 聚类 2#、7#和 8#, 主要关注玉米在高温胁迫下的生长表现和产量损失; 聚类 0#、1#和 6#, 主要关注玉米在高温胁迫下的生理响应; 聚类 4#和 5#, 主要关注玉米在高温胁迫下的分子机制; 聚类 8#、10#、11#、13#和 14#, 主要关注应对玉米高温胁迫的策略。

表 1　1990—2023 年玉米高温胁迫研究高频关键词

Table 1　High-frequency keywords of maize heat stress research from 1990 to 2023

关键词 Keyword	中心性 Centrality	频率 Frequency
Maize	0.23	1468
Heat stress	0.12	827
Yield	0.32	727
Growth	0.17	562
Stress	0.27	546
Temperature	0.32	535
Tolerance	0.36	420
Climate change	0.14	329
Expression	0.06	314
Plants	0.03	301
Oxidative stress	0.07	290
Drought	0.00	287
Responses	0.02	253
High temperature	0.21	248
Gene expression	0.28	241

3.2　玉米在高温胁迫下的生长表现和产量损失

过去 34 年间, 高温胁迫对玉米生长发育和产量的影响备受关注 (聚类 2#、7#和 8#)。不同生育阶段的高温胁迫对玉米的影响存在差异, 且多数研究仅侧重于某个时期, 故按苗期、穗期、花期和灌浆期分别回顾现有研究成果 (表 3)。

表 2　1990—2023 年玉米高温胁迫研究关键词聚类信息

Table 2　Keywords clustering information of maize heat stress research from 1990 to 2023

聚类 Cluster	规模 Size	轮廓值 Silhouette	主要关键词 Main keywords
0# Chlorophyll fluorescence	23	0.900	Chlorophyll fluorescence; cold stress; photoinhibition; chilling stress; photosynthesis
1# Oxidative stress	19	0.988	Oxidative stress; hydrogen peroxide; lipid peroxidation; antioxidant enzymes; ascorbate peroxidase
2# Heat stress	18	1.000	Heat stress; growth performance; heat tolerance; performance
3# High temperature	18	0.931	High temperature; stress; remote sensing; precipitation; model
4# Gene expression	17	0.983	Gene expression; expression; heat shock; arabidopsis; salt tolerance
5# Heat shock proteins	15	0.921	Heat shock proteins; heat shock protein; plants; tolerance; accumulation
6# Abscisic acid	14	0.937	Abscisic acid; leaves; water content; *zea-mays*; stress responses
7# Growth	14	0.895	Growth; *zea mays*; protein; quality; purification
8# Temperature	13	0.945	Temperature; grain yield; crop yield; yield; climate change
9# Rheology	13	1.000	Rheology; rice starch; viscosity; pasting properties; wheat starch
10# Water use efficiency	11	0.832	Water use efficiency; drought stress; ridge-furrow mulching system; temperature; non-water-stressed baseline
11# Abiotic stress	11	0.937	Abiotic stress; cold tolerance; low temperature; transgenic plants; drought tolerance
12# Water stress	11	0.935	Water stress; traits; genomic prediction; light interception; linkage disequilibrium
13# Canopy temperature	10	0.957	Canopy temperature; irrigation scheduling; management; decision support system; soil water
14# Climate change	10	1.000	Climate change; adaptation; food security; agriculture; *zea mays*

表 3　不同生育期高温胁迫对玉米生长发育和产量的影响

Table 3　Effects of heat stress on maize growth and yield at different growth stages

生育期 Growth stage	适宜温度 Optimal temperature (℃)	最高温度 Maximum temperature (℃)	生长表现 Growth performance	减产主因 Primary cause for yield reduction	产量损失率 Yield loss rate (%)
苗期 Seedling stage	28.3±3.8	39.2±0.6	1)发芽率下降, 出苗差; 2)植株瘦弱, 叶片枯黄早衰, 根系受损, 叶面积和生物量显著降低 1) Germination and emergence rates are decreased. 2) The plant is thin, leaves are yellow and premature, the roots are damaged, leaf area and biomass are significantly reduced	穗数↓ Ear number ↓	−4.9~6.1
穗期 Heading stage	28.3±3.8	39.2±0.6	1)光合速率降低, 生物量积累减少; 2)雌雄穗分化异常, 小花数减少; 3)开花-叶丝间隔增加 1) Photosynthetic rate and biomass accumulation decrease. 2) The differentiation of male and female spikes is abnormal, and the number of florets decreases. 3) The flowering-silking interval increases	穗粒数↓ Grains number per ear ↓	4.9~25.4
花期 Flowering stage	30.5±2.5	37.3±1.3	1)光合速率降低, 同化物供应不足, 运输受阻; 2)花粉、花丝活力下降, 授粉失败率增加; 3)选择性败育 1) The photosynthetic rate decreases, the supply of assimilates is insufficient, and the transport is blocked. 2) The vitality of pollen and filament decrease, and the failure rate of pollination increases. 3) Selective abortion	穗粒数↓ Grains number per ear ↓	12.8~68.5
灌浆期 Filling stage	26.4±2.1	36.0±1.4	1)灌浆速率加快, 灌浆时间缩短, 穗粒数和粒重下降; 2)叶片衰老, 生命周期缩短; 3)胚乳异常发育, 淀粉合成受阻 1) The grain filling rate is accelerated, the grain filling time is shortened, and the grains number per spike and grain weight are decreased. 2) Leaf senescence, shortened life cycle. 3) Endosperm abnormal development, blocked starch synthesis	粒重↓ Grain weight ↓	17.8~44.4

3.2.1　苗期高温

玉米种子萌发和幼苗生长对其后期生长具有重要影响[20-21]。玉米种子发芽的适宜温度为 26~29℃[22]。随着温度升高, 种子活力下降, 发芽率降低[22]。当温度超过 40℃ 时, 种子活力甚至完全丧失[23]。玉米幼苗在 26℃ 下生长最快, 每上升 1℃, 幼苗干重将减少 12%[24]。当超过 35℃ 时, 幼苗生长受到严重阻碍[24], 表现为植株瘦弱, 叶片枯黄, 根系受损, 叶面积和干物质显著降低[25-26]。与其他阶段相比, 苗期高温发生的可能性较低, 对产量的影响也很低[27]。研究[28-31] 发现, 经过硫化氢、Ca^{2+}和过氧化氢或其供体处理, 玉米幼苗能够保持较高的抗氧化酶活性, 从而提高耐热性。

3.2.2　穗期高温

玉米从播种到抽穗的适宜温度为 28.3℃, 最高温度为 39.2℃[32]。穗期的主要特征是根茎叶旺盛生长和雌雄穗强烈分化, 此阶段的干物质积累和穗发育对玉米产量具有重要影响[33-34]。穗期高温引起玉米减产的主要原因可概括为 3 点: 1) 高温对叶片造成损伤, 降低光合速率, 削弱物质生产能力, 从而减少干物质合成和积累[35]。还有研究[33] 表明, 七叶期至十叶期的干物质积累与穗长和小花数量呈正相关, 若此时遭受逆境胁迫, 将导致干物质积累受阻, 穗长变短, 小花数量损失。2) 高温引起雌雄穗分化异常, 导致小花数量和小花育性受到负面影响[36-37]。玉米在七叶期左右遭受高温胁迫, 穗行数形成将受到限制; 在雌穗萌芽到授粉期间遭受高温胁迫, 胚珠形成和发育将受到抑制, 秃尖现象加剧, 行粒数减少[37]。3) 高温对雌雄穗的影响程度不一致, 雄穗对高温更为敏感, 造成雌雄穗发育不同步, 进而使开花-吐丝间隔增大, 增加授粉失败的概率[38]。穗期高温导致的产量损失主要源于穗粒数的降低, 减产幅度为 4.9%~25.4%[39-40]。

3.2.3　花期高温

花期对高温最敏感。花期适宜温度为 30.5℃, 最高温度为 37.3℃[32]。花期高温主要通过影响穗发育、授粉、受精和结实等过程, 增加籽粒败育率, 最终导致产量损失[41]。穗粒数对花期高温的敏感度高于粒重, 而小花分化减少、授粉失败和籽粒败育是穗粒数降低的主要原因[41]。其中, 花粉四分体和授粉受精时期是花期对高温胁迫最脆弱的阶段[42]。在高温条件下, 花药和花粉粒发育异常, 花粉活力降低[43-44]。高温胁迫还会抑制花粉萌发和花粉管生长, 长时间暴露于 38℃ 的花粉无法萌发, 破坏受精过程[45]。有研究表明, 花期高温并不会引起光合活性的显著降低, 甚至促进营养器官生长, 但是减少了光合产物向雌穗的运输, 导致穗粒数降低和穗轴缩短[42]。在逆境胁迫下, 作物一般会通过牺牲顶部或基部的部分籽粒保证其余部位的籽粒正常发育。通常先受精的籽粒优先摄取同化物, 在籽粒竞争中占据优势; 而晚受精的籽粒在籽粒竞争中处于劣势, 究竟是通过自我调节而主动做出的牺牲, 还是受到先受精籽粒释放的信号抑制, 还需要更深入的研究[46]。除了影响授粉受精过程, 花期高温还会对籽粒灌浆过程产生持续

的影响[47]。过往研究表明, 花期高温造成的产量损失可达 12.8%~68.5%[39,48-50]。

3.2.4 灌浆期高温

玉米灌浆期适宜温度为 26.4℃, 最高温度为 36.0℃[32]。灌浆期是籽粒生物量积累的关键阶段, 粒重降低是此阶段产量下降的主要原因[51]。高温胁迫加快了灌浆速率, 但缩短了灌浆持续时间。灌浆速率增加无法弥补灌浆持续时间的损失, 从而对玉米产量造成负面影响[51-52]。这一结果主要源于胚乳在高温条件下的异常发育, 高温使得胚乳发育进程加速并提前终止[53]。同时, 叶片早衰也进一步缩短了灌浆持续时间[52]。此外, 高温还会降低淀粉合成关键酶活性及内源激素含量, 直接阻碍了籽粒淀粉合成和蔗糖积累[54]。Commuri 等[55] 研究也证实了这些观点, 他们发现随着高温胁迫时长的增加, 玉米胚乳细胞和淀粉颗粒数量逐渐减少, 进而导致籽粒干物质积累减少。灌浆期高温主要通过影响胚乳细胞分裂和淀粉合成, 引起粒重降低, 最终导致玉米的减产幅度为 17.8%~44.4%[27,56-57]。

3.3 玉米在高温胁迫下的生理响应

过去 34 年间, 高温胁迫对玉米生理生化特征的影响研究已成为研究重点, 特别关注光合作用 (聚类 0#)、氧化应激 (聚类 1#) 和激素调节 (聚类 6#) 这 3 方面 (图 1)。

3.3.1 光合作用受损

高温会明显破坏玉米叶片叶绿体结构, 导致光合作用受阻。光合作用在 30~35℃ 温度范围内基本保持稳定, 当叶片温度高于 38℃ 时, 净光合速率 (P_n) 显著降低[10]。高温胁迫加速叶绿素含量的降解, 其中叶绿素 b 的降幅高于叶绿素 a, 限制了光能捕获和利用[58]。光系统Ⅱ(PSⅡ) 在高温条件下光合活性受到抑制, 光合电子转移和 ATP 合成受阻, 而光系统Ⅰ不受抑制[59-61]。玉米 P_n 和气孔导度受高温影响降低, 但胞间 CO_2 浓度升高, 表明 P_n 降低与气孔闭合无关[60]。当温度高于 35℃ 时, 核酮糖 1,5-二磷酸羧化酶 (Rubisco) 等卡尔文循环相关酶活性降低, 进而减少光合碳同化[62-63]。相关研究认为, Rubisco 的失活是限制玉米 P_n 的主要因素[10]。

3.3.2 膜损伤和活性氧积累

生物膜是由脂质和蛋白质镶嵌组成的有序结构[64], 被认为是植物细胞中对高温最敏感的成分。生物膜上类脂分子的热致相变是高温逆境下产生不可逆伤害的原初反应[65]。高温胁迫引发脂质双层崩解和蛋白质变性, 膜流动性和透性增加, 导致生物膜的结构和功能受损[66]。细胞膜受损导致有机和无机离子外泄、有毒化合物生成和细胞内稳态失衡, 甚至细胞死亡。细胞膜和类囊体膜受损还会直接影响到植物光合作用和呼吸作用[67]。高温胁迫刺激活性氧 (ROS) 合成, 过度积累的 ROS 会对 DNA、RNA、蛋白质、酶类和脂类等生物大分子造成氧化损伤, 促进膜脂过氧化, 加剧生物膜受损, 导致细胞内容物泄漏[68]。膜脂过氧化最终生成的丙二醛, 是一种具有细胞毒性的物质, 其含量的高低可作为反映作物遭受逆境伤害程度的重要指标[69]。

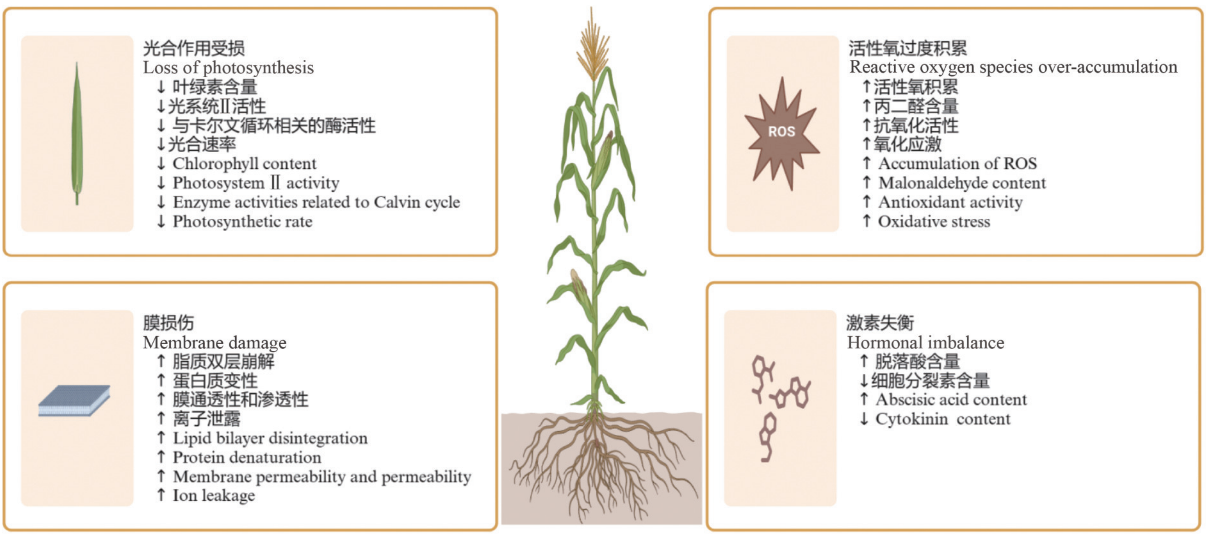

图 1 高温胁迫对玉米生理生化特征的影响

Fig. 1 Effects of heat stress on maize physiological and biochemical characteristics

图片使用 BioRender.com 创建。The figure was created with BioRender.com.

3.3.3 内源激素失衡

在非生物胁迫条件下, 生长素 (IAA)、赤霉酸 (GA)、脱落酸 (ABA)、细胞分裂素 (CTK)、茉莉酸 (JAs)、玉米素 (ZT) 和玉米素核苷 (ZR) 等激素在调节各项生理过程中具有重要作用[67-70]。在高温胁迫下, 玉米激素失衡, GA_3、GA_4 和 ABA 含量增加, ZT 和 ZR 含量降低, 导致幼穗小花数、小花受精率和穗粒数降低。高温胁迫还会显著降低玉米灌浆期的 IAA 含量, 并提高 ABA 含量[71]。高浓度的 ABA 通过转录调控加速叶片衰老, 并作为抑制剂对 PSⅡ受体的光能捕获和电子转移产生负面影响[72]。花期高温打破 JAs 和油菜素甾醇 (BRs) 的平衡, 浆片膨胀和小花开放异常, 导致授粉受阻[42]。研究发现, 高温胁迫破坏 ABA 和 CTK 之间的平衡是导致玉米籽粒发育不良的主要原因之一[73]。

3.4 玉米在高温胁迫下的分子机制

过去 34 年间, 玉米响应高温胁迫的分子机制受到研究人员的高度重视, 在基因表达和热休克蛋白运作方面取得了一定的进展 (聚类 4#和 5#)。

3.4.1 基因表达

高温胁迫能激活作物的内在保护机制, 触发一系列基因和蛋白质的表达, 以减轻细胞或生物体受热应激引起的损害。高温胁迫影响玉米 5000 多个基因的表达, 其中 2549 个基因上调, 2587 个基因下调[74], 然而, 具体的分子机制仍然知之甚少。李川等[75] 研究发现, 在玉米响应花粒期高温胁迫过程中, IAA 基因、磷脂酰基醇-4,5-二磷酸基因、热休克转录因子 (HSFs) 基因和热休克蛋白 (HSPs) 基因发挥着重要作用。在高温胁迫处理下, HSFA1 家族基因的表达显著增加。作为主调节因子, HSFA1 直接调控热休克反应基因 (*DREB2A*, *HSFA2*, *HSFA7a* 和 *HSFB* 等基因) 的表达, 进而增强玉米耐热性[76-77]。曹丽茹等[78] 研究表明, *ZmbZIP84* 基因在高温条件下表达显著上调, 起正向调控作用。敲除 *ZmHUG1* 基因的突变体在高温胁迫下表现出严重的内质网应激[79]。*OsMYB55* 基因过表达能够降低高温对玉米的负面影响, 促进玉米增产[80]。*ZmDnaJ96* 基因过表达可以提高叶绿体的抗氧化酶活性, 进而提高玉米耐热性[81]。Sprague 等[82] 研究报道, 在玉米中异源表达拟南芥 (*Arabidopsis thaliana*) *AtGRXS17* 基因能够显著提高玉米生殖阶段的耐热性, 从而保证较高的花粉活力和结实率。这些研究为培育耐热玉米品种提供了遗传资源。

3.4.2 热休克蛋白运作

HSPs 作为分子伴侣, 在高温胁迫或其他环境压力下会被诱导表达, 对维持蛋白质稳态、调控细胞免疫和凋亡等方面至关重要[83]。HSPs 按分子量大小可分为 HSP100、HSP90、HSP70、HSP60 和 sHSPs, 各自在细胞中发挥着不同或重叠的作用[83]。HSP21 存在于所有能进行光合作用的植物中, 是叶绿体发育的必需蛋白, 与 PSⅡ核心亚基蛋白结合能够增强高温下类囊体膜和 PSⅡ的稳定性, 减少光合作用受损[84-85]。sHSP26 的功能位点也在叶绿体内部, 通过与多个叶绿体蛋白互作, 可有效提升玉米叶绿体在高温胁迫环境下的性能, 提高玉米耐热性[86]。在减数分裂中, HSP101 的抗凋亡作用可有效保护雄性配子正常发育, 其过表达增强微孢子发生过程中的耐热性, 并提高高温下的花粉活力[87-88]。ZmHSP17.0-CII 和 ZmHSP17.8-CII 的蛋白质序列几乎一致, 但在热休克反应中存在显著差异, 前者优化玉米发育, 而后者是专门处理热损伤的客户蛋白[89]。

3.5 应对玉米高温胁迫的策略

过去 34 年间, 针对玉米高温胁迫的策略研究取得了显著进展, 明确指出农艺措施和育种技术是提高玉米耐热性的两大关键途径 (聚类 8#、10#、11#、13#和 14#)。

3.5.1 农艺措施

优化农艺管理措施, 包括调整播期、科学水肥管理及施用生长调节剂等, 是提高玉米耐热性、减轻高温胁迫影响的重要手段。调整播期以减少高温与玉米关键生长阶段的时间重叠, 是降低高温胁迫对玉米产量影响的有效策略[90]。在华北平原, 推迟玉米播期可以降低花粒期的温度, 减轻高温对穗粒数和粒重的不利影响[90]。Guo 等[91] 研究发现, 优化播期避免开花前后的高温胁迫, 能够提高玉米光合速率, 促进吐丝前后的干物质积累, 最终能实现玉米增产 11.2%~17.8%。当选用耐热品种并适期播种时, 甚至可以减轻约 80% 高温对玉米产量的影响[38]。

合理灌溉可以降低冠层温度并提高土壤含水量, 改善玉米生长环境, 进而提高玉米的耐热性[92-93]。灌溉能够直接降低玉米叶片温度, 还能通过蒸腾作用冷却植株, 延缓植株衰老, 延长有效灌浆期的持续时间[94-95]。灌溉还能提高叶绿素含量和 Rubisco 活性, 增加类囊体膜结构和功能的稳定性, 改善电子传递和质子梯度, 减轻光合作用的受损程度, 减少产量损失[94]。玉米遭受花期高温时, 喷灌能立即降低穗温, 并在 2 h 后降低冠层内气温, 减少生殖器官高温胁迫的持续时间, 同时还能降低受精失败的概率[96]。

科学施肥对于提高玉米对高温胁迫的适应能力

具有重要作用。在养分贫瘠的地区，通过施肥可以有效提升玉米对气候变暖的适应能力[97]。研究表明，将土壤全氮含量从 0.91 g·kg^{-1} 提高到 1.80 g·kg^{-1}，能够使春玉米在增温 1℃ 的情况下，从减产 10% 以上转变为增产[97]。增产原因可能是高氮植株相较于低氮植株具有更高的光合速率、更大的生物量，并且倾向于将更多的生物量分配给地上部分[98-99]。通过施加有机肥不仅能改善土壤肥力，提供玉米所需养分，还能增强土壤持水能力，增加土壤含水量，从而减轻高温热害的影响[100]。在高温干旱复合胁迫下，施用农家肥能够使玉米产量提高 10.5%~41.9%[101]。

适当应用生长调节剂是减轻高温胁迫对玉米伤害的有效手段。施用 ABA，可以提高 PSⅡ的能力，提高光合效率[102]。施用 $CaCl_2$，能够阻止 ROS 积累，增强抗氧化能力[103]。当同时施用 Ca^{2+}和 ABA 时，可以提高玉米幼苗的抗氧化酶活性，减少脂质过氧化[104-105]。苄基腺嘌呤的施用可以保持 ABA 和 CTK 之间的平衡，增加玉米幼苗的耐热性[73]。施用 BR，能够增加玉米小穗的张开角度和持续时间，这有利于散粉和授粉[106]。

3.5.2　育种技术

培育具有更强耐热性的新品种，能够从根本上提高玉米对高温胁迫的适应能力。耐热性的鉴定和筛选是育种过程中的重要环节[107]。生育期、积温需求、冠层结构、叶片气孔和光合速率等可作为耐热性指标[108]。一般来说，生育期长、积温需求高的玉米品种，往往展现出较强的耐热性，有助于缓解气候变暖对产量的负面影响[109-110]。针对花期高温，开花时间、花粉活力、小穗张开角度、花序结构和雌蕊生长状况等是重要的筛选指标[111]。常规育种通过选择具有优良耐热性的亲本进行杂交，进行多代的自交和选择，能够逐步稳定并增强玉米耐热性。然而，这种方法耗时较长且效率低。借助现代生物技术手段，如分子标记辅助育种和基因编辑育种等技术，可以提高育种效率，缩短育种时间。目前发现抗热性基因或数量性状位点 (QTL) 并将其应用于耐热育种是最为迫切的任务。已识别的 QTL 可以通过与 QTL 相连的 DNA 标记引入受体品种，以增强新品种的耐热性。

4　研究前沿

将玉米高温胁迫研究的关键词进行突现检测，得到 15 个突现关键词，其中“use efficiency” “soil” “food security”和“transcription factor”等突现词的热度持续至 2023 年 (表 4)，表明资源利用效率、土壤特性、粮食安全和转录因子是当前玉米高温胁迫研究的关注焦点及新兴趋势。

在玉米高温胁迫研究领域，HSFs 的相关研究被视为关键前沿，颇受关注。HSFs 在植物抵御高温胁迫以及其他非生物胁迫过程中发挥着关键的转录调控作用。植物通过调节 HSPs 合成以减轻热损伤，通过调控激素分泌以增强耐热性的过程，都与 HSFs 密切相关[112-113]。玉米拥有 30 个 HSFs，根据其特定结构可分为 3 个亚家族，即 A 类 16 个、B 类 9 个、C 类 5 个[114]。A 类 HSFs 具备转录激活因子的功能，对耐热性一般起到正调控作用，而 B、C 两类 HSFs 由于缺乏特定的蛋白质基序不具备此功能，可能作为与 A 类 HSFs 合作的共激活因子[115-116]。前人研究[116]发现，ZmHSF01、ZmHSF04、ZmHSF05、ZmHSF06 和 ZmHSF17 等 HSFs 正向调控耐热性，而 ZmHSF08、ZmHSF11、ZmHSF20 和 ZmHSF25 等 HSFs 则负向调控耐热性。ZmHSF05 过表达的株系存活率上升，叶绿素含量升高，HSPs 表达也呈增长趋势[117]。ZmHSF11 通过负调控氧化胁迫相关基因 (*APX2*、*DREB2A*、*HSFA2e*、*NTL3*、*GR* 和 *HSP17* 等基因) 的表达、增加 ROS 水平以及降低脯氨酸含量来降低植物对热胁迫的耐受性[118]。ZmHSF20 与 ZmHSF4 和纤维素合成酶基因 *ZmCesA2* 对玉米耐热性存在协同调控作用[119]。在 ZmHSF20 突变体中，ZmHSF4 和 ZmCesA2 的表达水平显著上升，促进了纤维素合成，增强了细胞壁稳定性，并提高了玉米耐热性[119]。Li 等[120] 研究发现玉米转录因子 bZIP60 能够将热休克反应与未折叠蛋白反应联系起来，为玉米耐热性研究提供了新的思路和靶点基因。

5　结论

随着气候变暖的加剧，玉米高温胁迫已成为世界各国关注的焦点。全球玉米高温胁迫研究主要集中在 4 个核心方面：一是探究玉米在高温胁迫下的生长表现和产量损失，各生育阶段受高温胁迫造成的玉米减产幅度表现为花期>灌浆期>穗期>苗期；二是探究高温胁迫对玉米的生理响应，包括光合作用受损、膜损伤和活性氧积累、激素失衡等；三是探究玉米响应高温胁迫的分子机制，尤其关注基因表达和热休克蛋白运作，但具体机制仍未明晰；四是探究应对玉米高温胁迫的策略，优化农艺措施和培育耐热品种被认为是两大关键手段。特别值得一提的是，热休克转录因子作为玉米响应高温胁迫的关键

表 4 1990—2023 年玉米高温胁迫研究突现关键词

Table 4 Burst words of high temperature stress studies in maize from 1990 to 2023

关键词 Keyword	突现强度 Strength	持续时间 Duration	1990—2023
Maize	45.98	1991—2007	
Higher plants	9.08	1991—2001	
Chlorophyll fluorescence	18.95	1997—2009	
Photosystem Ⅱ	11.40	1997—2005	
Photoinhibition	10.99	1997—2009	
Hydrogen peroxide	29.32	1999—2012	
Maize seedlings	26.27	1999—2013	
Oxidative stress	15.32	1999—2012	
Superoxide dismutase	14.83	1999—2012	
Arabidopsis thaliana	11.40	2001—2009	
Low temperature	18.09	2002—2011	
Chilling tolerance	9.20	2004—2011	
Accumulation	12.62	2006—2011	
Cold stress	9.08	2008—2011	
Quantitative trait loci	8.77	2009—2014	
Leaves	8.20	2009—2013	
Arabidopsis	7.85	2010—2014	
Crop production	8.93	2016—2018	
Use efficiency	8.19	2017—2023	
Management	7.91	2017—2020	
Variability	10.12	2019—2021	
Evapotranspiration	9.81	2019—2021	
Soil	11.17	2020—2023	
Food security	8.66	2021—2023	
Transcription factor	7.84	2021—2023	

组分, 近年来相关研究激增, 已成为该领域的研究前沿。

参考文献 References

[1] GISTEMP Team. GISS Surface Temperature Analysis (GISTEMP), version 4[EB/OL]. Washington: NASA Goddard Institute for Space Studies, [2024/2/22]. https://data.giss.nasa.gov/gistemp

[2] LENSSEN N G, SCHMIDT J, HANSEN M, et al. Improvements in the GISTEMP uncertainty model[J]. Journal of Geophysical Research: Atmospheres, 2019, 124: 6307−6326

[3] IPCC. Climate Change 2021: The Physical Science Basis[M]. New York: Cambridge University Press, 2021

[4] ZHAO C, LIU B, PIAO S L, et al. Temperature increase reduces global yields of major crops in four independent estimates[J]. Proceedings of the National Academy of Sciences of the United States of America, 2017, 114(35): 9326−9331

[5] BITA C E, GERATS T. Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops[J]. Frontiers in Plant Science, 2013, 4: 273

[6] SHIFERAW B, PRASANNA B M, HELLIN J, et al. Crops that feed the world 6. Past successes and future challenges to the role played by maize in global food security[J]. Food Security, 2011, 3: 307−327

[7] FAO. World Food and Agriculture-Statistical Yearbook 2023[M]. Rome: Food and Agriculture Organization of the United Nations Press, 2023

[8] TAS T. Physiological and biochemical responses of hybrid maize (*Zea mays* L.) varieties grown under heat stress conditions[J]. PeerJ, 2022, 10(21): e14141

[9] 中华人民共和国国家统计局. 国家统计局关于 2023 年粮食产量数据的公告[EB/OL]. 北京: 国家统计局, 2023 (2023-12-11)[2024-02-04]. https://www.stats.gov.cn/sj/zxfb/202312/t20231211_1945417.html

National Bureau of Statistics of the People's Republic of China. Announcement of the National Bureau of Statistics of the People's Republic of China on grain production data for 2023[EB/OL]. Beijing: National Bureau of Statistics, 2023 (2023-12-11)[2024-02-04]. https://www.stats.gov.cn/sj/zxfb/202312/t20231211_1945417.html
[10] CRAFTS-BRANDNERS S J, SALYUCCi M E. Sensitivity of photosynthesis in a C4 plant, maize, to heat stress[J]. Plant Physiology, 2002, 129(4): 1773–1780
[11] GOURDJI S M, SIBLEY A M, LOBELL D B, et al. Global crop exposure to critical high temperatures in the reproductive period: historical trends and future projections[J]. Environmental Research, 2013, 8(2): 024041
[12] HU J, ZHAO X Y, GU L M, et al. The effects of high temperature, drought, and their combined stresses on the photosynthesis and senescence of summer maize[J]. Agricultural Water Management, 2023, 289: 108525
[13] SINGLETARY G W, BANISADR R, KEELING P L. Heat stress during grain filling in maize: effects on carbohydrate storage and metabolism[J]. Function Plant Biology, 1994, 21(6): 829−841
[14] HUSSAIN H A, MEN S N, HUSSAIN S, et al. Interactive effects of drought and heat stresses on morpho-physiological attributes, yield, nutrient uptake and oxidative status in maize hybrids[J]. Scientific Reports, 2019, 9(1): 3890
[15] WAHID A, GELANI S, ASHRAF M, et al. Heat tolerance in plants: An overview[J]. Environmental and Experimental Botany, 2007, 61(3): 199−223
[16] FENG L, TANG H Y, PU T, et al. Maize-soybean intercropping: A bibliometric analysis of 30 years of research publications[J]. Agronomy Journal, 2022, 114(6): 3377−3388
[17] CHEN C M. CiteSpace Ⅱ: detecting and visualizing emerging trends and transient patterns in scientific literature[J]. Journal of the American Society for Information Science and Technology, 2006, 57(3): 359−377
[18] ZHONG D L, LI Y X, HUANG Y J, et al. Molecular mechanisms of exercise on cancer: A bibliometrics study and visualization analysis via CiteSpace[J]. Frontiers in Molecular Biosciences, 2022, 8: 797902
[19] 陈悦, 陈超美, 刘则渊, 等. CiteSpace 知识图谱的方法论功能[J]. 科学学研究, 2015, 33(2): 242−253
CHEN Y, CHEN C M, LIU Z Y, et al. The methodology function of CiteSpace mapping knowledge domains[J]. Studies in Science of Science, 2015, 33(2): 242−253
[20] XUE X F, DU S Y, JIAO F C, et al. The regulatory network behind maize seed germination: Effects of temperature, water, phytohormones, and nutrients[J]. The Crop Journal, 2021, 9: 901−904
[21] ELLIS R H. Seed and seedling vigour in relation to crop growth and yield[J]. Plant Growth Regulation, 1992, 11(3): 249−255
[22] RILEY G. Effects of high temperature on the germination of maize (*Zea mays* L.)[J]. Planta, 1981, 151(1): 68−74
[23] KHAEIM H M, KENDE ZENDE Z, JOLANKAI M, et al. Impact of temperature and water on seed germination and seedling growth of maize (*Zea mays* L.)[J]. Agronomy, 2022, 12(2): 397
[24] WALKER J M. One-degree increments in soil temperatures affect maize seedling behavior[J]. Soil Science Society of America Journal, 2024, 88(1): 729−736
[25] CICCHINO M A, EDREIRA J I R, OTEGUI M E. Maize physiological responses to heat stress and hormonal plant growth regulators related to ethylene metabolism[J]. Crop Science, 2013, 53(5): 2135–2146
[26] WANG Q, XIA Z Q, ZHANG S B, et al. Elevated temperature during seedling stage in different maize varieties: Effect on seedling growth and leaf physiological characteristics[J]. Russian Journal of Plant Physiology, 2022, 69(6): 1
[27] 张保仁. 高温对玉米产量和品质的影响及调控研究[D]. 泰安: 山东农业大学, 2003
ZHANG B R. Studies on effect of high temperature on yield and quality and regulation in maize (*Zea Mays* L.)[D]. Tai'an: Shandong Agricultural University, 2003
[28] LI Z G, XIE L R, LI X J. Hydrogen sulfide donor sodium hydrosulfide-improved heat tolerance in maize and involvement of proline[J]. Journal of Plant Physiology, 2013, 177: 121−127
[29] LI Z G, YI X Y, LI Y T. Effect of pretreatment with hydrogen sulfide donor sodium hydrosulfide on heat tolerance in relation to antioxidant system in maize (*Zea mays*) seedlings[J]. Biologia, 2014, 69: 1001−1009
[30] GONG M, CHEN S N, SONG Y Q, et al. Effect of calcium and calmodulin on intrinsic heat tolerance in relation to antioxidant systems in maize seedlings[J]. Australian Journal of Plant Physiology, 2003, 24(3): 371−379
[31] GONG M, CHEN B, LI Z G, et al. Heat-shock-induced cross adaptation to heat, chilling, drought and salt stress in maize seedlings and involvement of H_2O_2[J]. Journal of Plant Physiology, 2001, 158(9): 1125−1130
[32] SANCHEZ B, RASMUSSEN A M H, PORTER J R. Temperatures and the growth and development of maize and rice: A review[J]. Global Change Biology, 2013, 20(2): 408−417
[33] GONZALEZ V H, LEE E A, LUKENS L, et al. The relationship between floret number and plant dry matter accumulation varies with early season stress in maize (*Zea mays* L.)[J]. Field Crops Research, 2019, 238: 129−138
[34] LIU P, YIN B Z, GU L M, et al. Heat stress affects tassel development and reduces the kernel number of summer maize[J]. Frontiers in Plant Science, 2023, 14: 1186921
[35] 马昕, 蔡丰乐, 穆心愿, 等. 施氮量对穗期高温胁迫下玉米叶片光合生理及产量的影响[J]. 植物营养与肥料学报, 2022, 28(10): 1852−1866
MA X, CAI F L, MU X Y, et al. Effects of nitrogen application rate on photosynthetic physiology of maize leaves and yield under high temperature stress at ear stage[J]. Journal of Plant Nutrition and Fertilizers, 2022, 28(10): 1852−1866
[36] BEGCY K, NOSENKO T, ZHOU L Z, et al. Male sterility in maize after transient heat stress during the tetrad stage of pollen development[J]. Plant Physiology, 2019, 181: 683−700

[37] STRACHAN S D. Corn grain yield in relation to stress during ear development[EB/OL]. Iowa: Poineer, 2019(2019-05-14) [2024-02-22]. https://www.pioneer.com/us/agronomy/ear_development.html

[38] LIU M Y, DONG X, ZHANG Y J, et al. Heat stress on maize with contrasting genetic background: Differences in flowering and yield formation[J]. Agricultural and Forest Meteorology, 2022, 319: 108934

[39] SIEBERS M H, SLATTERY R A, YENDREK C R, et al. Simulated heat waves during maize reproductive stages alter reproductive growth but have no lasting effect when applied during vegetative stages[J]. Agriculture, Ecosystems & Environment, 2017, 240: 162–170

[40] 付景, 孙宁宁, 刘天学, 等. 穗期高温对玉米子粒灌浆生理及产量的影响[J]. 作物杂志, 2019(3): 118−125
FU J, SU N N, LIU T X, et al. The effects of high temperature at spike stage on grain-filling physiology and yield of maize[J]. Crops, 2019(3): 118−125

[41] EDREIRA J I R, CARPICI E B, SAMMARRO D, et al. Heat stress effects around flowering on kernel set of temperate and tropical maize hybrids[J]. Field Crops Research, 2011, 123(2): 62−73

[42] SUWA R, HAKATA H, HARA H, et al. High temperature effects on photosynthate partitioning and sugar metabolism during ear expansion in maize (*Zea mays* L.) genotypes[J]. Plant Physiology and Biochemistry, 2010, 48: 124−130

[43] LIZASO J I, RUIZ-RAMOS M, RODRIGUEZ L, et al. Impact of high temperatures in maize: Phenology and yield components[J]. Field Crops Research, 2018, 216: 129−140

[44] HERRERO M P, JOHNSON R R. High temperature stress and pollen viability of maize[J]. Crop Science, 1980, 20: 796−800

[45] DUPUIS I, DUMAS C. Influence of temperature stress on *in vitro* fertilization and heat shock protein synthesis in maize (*Zea mays* L.) reproductive tissues[J]. Plant Physiology, 1990, 94: 665−670

[46] SHEN S, MA S, WU L M, et al. Winners take all: Competition for carbon resource determines grain fate[J]. Trends in Plant Science, 2023, 28(8): 893−901

[47] LIU X W, YU Y H, HUANG S B, et al. The impact of drought and heat stress at flowering on maize kernel filling: Insights from the field and laboratory[J]. Agricultural and Forest Meteorology, 2022, 312: 108733

[48] WANG Y Y, LIU X L, HOU X F, et al. Maximum lethal temperature for flowering and seed set in maize with contrasting male and female flower sensitivities[J]. Journal of Agronomy and Crop Science, 2021, 207(4): 1−11

[49] 赵龙飞, 李潮海, 刘天学, 等. 花期前后高温对不同基因型玉米光合特性及产量和品质的影响[J]. 中国农业科学, 2012, 45(23): 4947−4958
ZHAO L F, LI C H, LIU T X, et al. Effect of high temperature during flowering on photosynthetic characteristics and grain yield and quality of different genotypes of maize (*Zea Mays* L.)[J]. Scientia Agricultura Sinica, 2012, 45(23): 4947−4958

[50] NICOLAS N, TRACHSEL S, VALENTINUZ O R, et al. High temperatures around flowering in maize: Effects on photosynthesis and grain yield in three genotypes[J]. Crop Science, 2016, 56(5): 2081−2869

[51] CAO Z Y, CHEN Z H, TANG B, et al. The effects of sowing date on maize: Phenology, morphology, and yield formation in a hot subtropical monsoon region[J]. Field Crops Research, 2024, 309: 109309

[52] JONES R J, GENENBACH B G, CARDWELL V B. Temperature effects on *in vitro* kernel development of maize[J]. Crop Science, 1981, 21(5): 761−766

[53] BOEHLEIN S K, LIU P, WEBSTER A, et al. Effects of long-term exposure to elevated temperature on *Zea mays* endosperm development during grain fill[J]. The Plant Journal, 2019, 99(1): 23−40

[54] 张桂莲, 廖斌, 武小金, 等. 高温对水稻胚乳淀粉合成关键酶活性及内源激素含量的影响[J]. 植物生理学报, 2014, 50(12): 1840−1844
ZHANG G L, LIAO B, WU X J, et al. Effect of high temperature on activities of enzymes associated with starch synthesis and hormones contents in endosperm of rice[J]. Plant Physiology Journal, 2014, 50(12): 1840−1844

[55] COMMURI P D, JONES R J. Ultrastructural characterization of maize (*Zea mays* L.) kernels exposed to high temperature during endosperm cell division[J]. Plant, Cell and Environment, 1999, 22: 375−385

[56] 余梦奇, 路梦莉, 张雅婷, 等. 灌浆期高温对玉米叶片光合特性及抗氧化酶活性的影响[J]. 中国农业气象, 2023, 44(7): 599−610
YU M Q, LU M L, ZHANG Y T, et al. Effects of high temperature on photosynthetic characteristics and antioxidant enzyme activities of maize leaves during filling stage[J]. Chinese Journal of Agrometeorology, 2023, 44(7): 599−610

[57] BADUAPRAKU B, HUNTER R B, TOLLENAAR M. Effect of temperature during grain filling on whole plant and grain yield in maize (*Zea mays* L.)[J]. Canadian Journal of Plant Science, 1983, 63(2): 357−363

[58] SINGH I, DEBNATH S, GAUTAM A, et al. Characterization of contrasting genotypes reveals general physiological and molecular mechanisms of heat-stress adaptation in maize (*Zea mays* L.)[J]. Physiology and Molecular Biology of Plants, 2020, 26(5): 921−929

[59] SHARKEY T D, ZHANG R. High temperature effects on electron and proton circuits of photosynthesis[J]. Journal of Integrative Plant Biology, 2010, 52(8): 712−722

[60] LI Y T, XU W W, REN B Z, et al. High temperature reduces photosynthesis in maize leaves by damaging chloroplast ultrastructure and photosystem Ⅱ[J]. Journal of Agronomy and Crop Science, 2020, 206(5): 548−564

[61] GUIDI L, PICCOLO E L, LANDI M. Chlorophyll fluorescence, photoinhibition and abiotic stress: Does it make any difference the fact to be a C3 or C4 species?[J]. Frontiers in Plant Science, 2019, 10: 174

[62] YU H D, YANG X F, CHEN S T, et al. Down regulation of chloroplast RPS1 negatively modulates nuclear heat-responsive expression of HSFA2 and its target genes in arabidopsis[J]. PLOS Genetics, 2012, 8(5): e1002669

[63] CRAFTS-BRANDNERS S J, LAW R D. Effect of heat stress on the inhibition and recovery of the ribulose-1, 5-bisphosphate carboxylase/oxygenase activation state[J]. Planta, 2000, 212: 67−74
[64] NIU Y, YUN X. An overview of biomembrane functions in plant responses to high-temperature stress[J]. Frontiers in Plant Science, 2018, 9: 915
[65] LYONS J M. Chilling injury in plants[J]. Annual Review of Plant Biology, 1973, 24: 445−466
[66] HIGASHI Y, SAITO K. Lipidomic studies of membrane glycerolipids in plant leaves under heat stress[J]. Progress in Lipid Research, 2019, 75: 100990
[67] BARNABAS B, JAGER K, FEHER A. The effect of drought and heat stress on reproductive processes in cereals[J]. Plant, Cell and Environment, 2008, 31: 11−38
[68] BANERJEE A, ROYCHOUDHURY A. Abiotic stress, generation of reactive oxygen species, and their consequences[M]//SINGH V P, SINGH S, TRIPATHI D, et al. Reactive Oxygen Species in Plants: Boon or Bane-Revisiting the Role of ROS. New Jersey: John Wiley & Sons Ltd, 2018: 23–50
[69] PAMPLONA R. Membrane phospholipids, lipoxidative damage and molecular integrity: A causal role in aging and longevity[J]. Biochimica et Biophysica Acta (BBA)-Bioenergetics, 2008, 1777: 1249−1262
[70] SHARMA A, SHAHZAD B, KUMAR V, et al. Phytohormones regulate accumulation of osmolytes under abiotic stress[J]. Biomolecules, 2019, 9: 285
[71] QU L L, GU X T, LI J, et al. Leaf photosynthetic characteristics of waxy maize in response to different degrees of heat stress during grain filling[J]. BMC Plant Biology, 2023, 23(1): 469
[72] CHEN K, LI G J, BRESSAN R A, et al. Abscisic acid dynamics, signaling, and functions in plants[J]. Journal of Integrative Plant Biology, 2019, 62(1): 25−54
[73] CHEIKH N, JONES R J. Disruption of maize kernel growth and development by heat stress (role of cytokinin/abscisic acid balance)[J]. Plant Physiology, 1994, 106: 45−51
[74] JOSHI J, HASNAIN G, LOGUE T, et al. A core metabolome response of maize leaves subjected to longduration abiotic stresses[J]. Metabolites, 2021, 11(11): 797
[75] 李川, 乔江方, 朱卫红, 等. 玉米自交系响应花粒期高温胁迫差异表达基因的分析[J]. 华北农学报, 2019, 34(1): 1−11
LI C, QIAO J F, ZHU W H, et al. Differential expression of high temperature stress in anthesis stage related genes of maize inbred lines[J]. Acta Agriculturae Boreali-Sinica, 2019, 34(1): 1−11
[76] LIU H C, LIAO H T, CHARNG Y Y. The role of class A1 heat shock factors (HSFA1s) in response to heat and other stresses in *Arabidopsis*[J]. Plant Cell Environment, 2011, 34: 738−751
[77] YOSHIDA T, OHAMA N, NAKAJIMA J, et al. *Arabidopsis* HsfA1 transcription factors function as the main positive regulators in heat shock-responsive gene expression[J]. Molecular Genetics and Genomics, 2011, 286(5-6): 321−332
[78] 曹丽茹, 庞芸芸, 叶飞宇, 等. 玉米逆境胁迫响应基因 *ZmbZIP84* 的克隆与功能验证[J]. 核农学报, 2024, 38(4): 644–653
CAO L R, PANG Y Y, YE F Y, et al. Cloning and functional verification of maize stress response gene *ZmbZIP84*[J]. 2024, 38(4): 644–653
[79] XIE C, YANG L, JIA G X, et al. Maize heat up-regulated gene 1 plays vital roles in heat stress tolerance[J]. Journal of Experimental Botany, 2022, 73(18): 6417−6433
[80] CASARETTO J A, EL-KEREAMY A, ZENG B, et al. Expression of *OsMYB55* in maize activates stress-responsive genes and enhances heat and drought tolerance[J]. BMC Genomics, 2016, 17: 312
[81] CAO L R, WANG G R, FAHIM A M, et al. Comprehensive analysis of the *DnaJ/HSP40* gene family in maize (*Zea mays* L.) reveals that *ZmDnaJ96* enhances abiotic stress tolerance[J]. Journal of Plant Growth Regulation, 2024, 43: 1548−1569
[82] SPRAGUE S A, TAMANG T M, STEINER T, et al. Redox-engineering enhances maize thermotolerance and grain yield in the field[J]. Plant Biotechnology Journal, 2022, 20(9): 1819−1832
[83] AL-WHAIBI M H. Plant heat-shock proteins: A mini review[J]. Journal of King Saud University-Science, 2011, 23(2): 139−150
[84] ZHONG L L, WEN Z, WANG H J, et al. Chloroplast small heat shock protein HSP21 interacts with plastid nucleoid protein pTAC5 and is essential for chloroplast development in Arabidopsis under heat stress[J]. Plant Cell, 2013, 25: 2925−2943
[85] CHEN S T, HE N Y, CHEN J H, et al. Identification of core subunits of photosystem Ⅱ as action sites of HSP21, which is activated by the GUN5-mediated retrograde pathway in Arabidopsis[J]. The Plant Cell, 2016, 89(6): 1106−1118
[86] HU X L, YANG Y F, GONG F P, et al. Protein sHSP26 improves chloroplast performance under heat stress by interacting with specific chloroplast proteins in maize (*Zea mays*)[J]. Journal of Proteomics, 2015, 115: 81–92
[87] SOTTILE M L, NADIN S B. Heat shock proteins and DNA repair mechanisms: An updated overview[J]. Cell Stress Chaperones, 2018, 23: 303–315
[88] LI Y F, HUANG Y M, SUN H Y, et al. Heat shock protein 101 contributes to the thermotolerance of male meiosis in maize[J]. The Plant Cell, 2022, 34(10): 3702−3717
[89] KLEIN R D, CHIDAWANYIKA T, TIMS H S, et al. Chaperone function of two small heat shock proteins from maize[J]. Plant Science, 2014, 221/222: 48–58
[90] ZHANG X P, CHENG J L, WANG B, et al. Optimum sowing dates for high-yield maize when grown as sole crop in the North China Plain[J]. Agronomy. 2019, 9(4): 198
[91] GUO D, CHEN C Y, LI X L, et al. Adjusting sowing date improves the photosynthetic capacity and grain yield by optimizing temperature condition around flowering of summer maize in the North China Plain[J]. Frontiers in Plant Science, 2022, 13: 934618
[92] SIEBERT S, WEBBER H, ZHAO G, et al. Heat stress is overestimated in climate impact studies for irrigated

agriculture[J]. Environmental Research Letters, 2017, 12(5): 054023
[93] WANG X L, LUO N, ZHU Y P, et al. Water replenishment to maize under heat stress improves canopy temperature and grain filling traits during the reproductive stage[J]. Agricultural and Forest Meteorology, 2023, 340: 109627
[94] WANG X L, ZHU Y P, YAN Y, et al. Irrigation mitigates the heat impacts on photosynthesis during grain filling in maize[J]. Journal of Integrative Agriculture, 2023, 22(8): 2370–2383
[95] ZHU P, BURNEY J. Untangling irrigation effects on maize water and heat stress alleviation using satellite data[J]. Hydrology and Earth System Sciences, 2022, 26: 827–840
[96] JIAN H J, GAO Z, GUO Y Y, et al. Supplemental irrigation mitigates yield loss of maize through reducing canopy temperature under heat stress[J]. Agricultural Water Management, 2024, 299: 108888
[97] DENG X, HUANG Y, QIN Z C. Soil indigenous nutrients increase the resilience of maize yield to climatic warming in China[J]. Environmental Research Letters, 2020, 15(9): 094047
[98] ZHAO D L, REDDY K, KAKANI V G, et al. Corn (*Zea mays* L.) growth, leaf pigment concentration, photosynthesis and leaf hyperspectral reflectance properties as affected by nitrogen supply[J]. Plant and Soil, 2003, 257: 205−218
[99] CHEN J W, YANG Z Q, ZHOU P, et al. Biomass accumulation and partitioning, photosynthesis, and photosynthetic induction in field-grown maize (*Zea mays* L.) under low- and high-nitrogen conditions[J]. Acta Physiologiae Plantarum, 2013, 35: 95−105
[100] OUATTARA K, OUATTARA B, SEDOGO P M. Long-term effect of ploughing, and organic matter input on soil moisture characteristics of a Ferric Lixisol in Burkina Faso[J]. Soil and Tillage Research, 2006, 88(1-2): 217−224
[101] GAEVAYA E, ILYINSKAYA I, BEZUGLOVA O, et al. Influence of heat stress and water availability on productivity of silage maize (*Zea mays* L.) under different tillage and fertilizer management practices in Rostov Region of Russia[J]. Agronomy, 2023, 13(2): 320
[102] GONG M, LI Y J, DAI X, et al. Involvement of calcium and calmodulin in the acquisition of heat-shock induced thermotolerance in maize seedlings[J]. Journal of Plant Physiology, 1997, 150: 615−621
[103] TAO F, ZHANG Z. Adaptation of maize production to climate change in North China Plain: quantify the relative contributions of adaptation options[J]. European Journal of Agronomy, 2010, 33: 103−116
[104] HOSSAIN M A, BHATTACHARJEE S, ARMIN S M, et al. Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: insights from ROS detoxification and scavenging[J]. Frontiers in Plant Science, 2015, 6: 420
[105] YANG L J, WANG Y F, YANG K J. Klebsiella variicola improves the antioxidant ability of maize seedlings under saline-alkali stress[J]. PeerJ, 2021, 9: e11963
[106] LIU X L, GU M Q, LV X L, et al. High temperature defense pathways mediate lodicule expansion and spikelet opening in maize tassels[J]. Journal of Experimental Botany, 2023, 74(12): 3684–3699
[107] GONG F P, WU X L, ZHANG H Y, et al. Making better maize plants for sustainable grain production in a changing climate[J]. Frontiers in Plant Science, 2015, 6: 835
[108] SAH R, CHAKRABORTY M, PRASAD K, et al. Impact of water deficit stress in maize: phenology and yield components[J]. Scientific Reports, 2020, 10: 2944
[109] XIAO D P, QI Y Q, SHEN Y J, et al. Impact of warming climate and cultivar change on maize phenology in the last three decades in North China Plain[J]. Theoretical and Applied Climatology, 2016, 124: 653−661
[110] LIU Z J, HUBBARD K G, LIN X M, et al. Negative effects of climate warming on maize yield are reversed by the changing of sowing date and cultivar selection in Northeast China[J]. Global Change Biology, 2013, 19(11): 3481−3492
[111] LIU M Y, ZHOU Y H, SUN J X, et al. From the floret to the canopy: High temperature tolerance during flowering[J]. Plant Communications, 2023, 4(6): 100629
[112] ALI S, RIZWAN M, ARIF M S, et al. Approaches in enhancing thermotolerance in plants: An updated review[J]. Plant Growth Regul, 2020, 39(1): 456–480
[113] KAN Y, MU X R, GAO J, et al. The molecular basis of heat stress responses in plants[J]. Molecular Plant, 2023, 16(10): 1612−1634
[114] SCHARF K D, BERBERICH T, EBERSBERGER I, et al. The plant heat stress transcription factor (Hsf) family: structure, function and evolution[J]. Biochim Biophys Acta, 2012, 1819(2): 104−119
[115] DORING P, TREUTER E, KISTNER C, et al. The role of AHA motifs in the activator function of tomato heat stress transcription factors HsfA1 and HsfA2[J]. Plant Cell, 2000, 12(2): 265−278
[116] RUAN M X, ZHAO H, WEN Y J, et al. The complex transcriptional regulation of heat stress response in maize[J]. Stress Biology, 2024, 4: 24
[117] LI G L, ZHANG H N, SHAO H, et al. ZmHsf05, a new heat shock transcription factor from *Zea mays* L. improves thermotolerance in *Arabidopsis thaliana* and rescues thermotolerance defects of the athsfa2 mutant[J]. Plant Science, 2019, 283: 375−384
[118] QIN Q Q, ZHAO Y J, ZHANG J J, et al. A maize heat shock factor ZmHsf11 negatively regulates heat stress tolerance in transgenic plants[J]. BMC Plant Biology, 2022, 22: 406
[119] LI Z, LI Z R, JI Y L, et al. The heat shock factor 20-HSF4-cellulose synthase A2 module regulates heat stress tolerance in maize[J]. The Plant Cell, 2024, koae106
[120] LI Z, TANG J, SRIVASTAVA R, et al. The transcription factor BZIP60 links the unfolded protein response to the heat stress response in maize[J]. The Plant Cell, 2020, 32(11): 3559−3575