第 35 卷 第 11 期
Vol. 35, No. 11
草 业 学 报
ACTA PRATACULTURAE SINICA
145－156
2026 年 11 月

DOI: 10. 11686/cyxb2025454
http://cyxb. magtech. com. cn

葛秋岑, 祁虹银, 李州. 短期热胁迫对不同耐热型匍匐翦股颖品种可溶性糖与脂质变化的影响. 草业学报, 2026, 35(11): 145－156.
GE Qiu-cen, QI Hong-yin, LI Zhou. Effects of short-term heat stress on the contents of soluble sugars and lipids in creeping bentgrass cultivars with different degrees of heat tolerance. Acta Prataculturae Sinica, 2026, 35(11): 145－156.

短期热胁迫对不同耐热型匍匐翦股颖品种可溶性糖与脂质变化的影响

葛秋岑**, 祁虹银**, 李州*
(四川农业大学草业科技学院, 四川 成都 611130)

摘要: 夏季高温胁迫不仅抑制了草坪草的正常生长发育, 也增加了草坪养护管理成本。选取匍匐翦股颖耐热品种13M和热敏感品种Seaside Ⅱ为试验材料, 研究在38 ℃的短期高温胁迫下两个不同耐热品种叶片内脂质成分和可溶性糖含量的差异变化, 以期揭示不同耐热型匍匐翦股颖快速响应热胁迫的策略。研究结果显示, 3 h的短期高温胁迫未引起两个品种叶片内果糖含量的显著变化, 但显著提高了13M体内蔗糖的含量, 而Seaside Ⅱ则显著增加了葡萄糖的积累。脂质组分析发现, 短期热胁迫下热敏型材料Seaside Ⅱ体内的总脂质、磷脂、糖脂和鞘脂含量均显著下降, 而耐热型品种13M的总脂质和鞘脂含量保持不变, 磷脂含量有所上升, 仅糖脂含量显著下降。耐热品种13M在短期高温胁迫下比热敏感品种Seaside Ⅱ积累了更多的总脂质、糖脂(磺基奎诺糖基单酰基甘油、单半乳糖基二酰基甘油、单半乳糖基单酰基甘油)、磷脂(磷脂酸、磷脂酰肌醇磷酸酯、溶血磷脂酰丝氨酸、溶血磷脂酰肌醇、溶血磷脂酰甘油、单溶血心磷脂)和鞘脂(二己糖基N-乙酰基己糖基神经酰胺、磷酸神经酰胺、二己糖神经酰胺、三己糖神经酰胺), 这有利于热胁迫下13M保持较好的细胞膜完整性与稳定性, 维持细胞正常功能。此外, 在磷脂信号通路中13M与Seaside Ⅱ表现出了不同的高温响应策略, 13M主要通过促进磷脂酸(PA)的积累, 而Seaside Ⅱ则主要通过提高磷脂酰肌醇(PI)和磷脂酰肌醇三磷酸(PIP3)的合成以响应短期热胁迫。这些研究结果表明, 耐热型不同的13M和Seaside Ⅱ在响应短期热胁迫时脂质和糖代谢有所不同, 13M通过维持较高的脂质含量和脂质信号物质以增强自身耐热性。这些研究结果为改良冷季型草坪草的耐热性提供了新的思路。然而, 13M和Seaside Ⅱ的耐热性差异是否与促进脂－糖转化有关仍需进一步深入研究。

关键词: 匍匐翦股颖; 高温胁迫; 脂质代谢; 蔗糖; 果糖; 葡萄糖

Effects of short-term heat stress on the contents of soluble sugars and lipids in creeping bentgrass cultivars with different degrees of heat tolerance

GE Qiu-cen**, QI Hong-yin**, LI Zhou*
College of Grassland Science and Technology, Sichuan Agricultural University, Chengdu 611130, *China*

Abstract: High temperature stress in summer not only inhibits the normal growth and development of turfgrass, but also increases the cost of turf maintenance and management. In this study, we compared the responses of a heat-tolerant cultivar (13M) and heat-sensitive cultivar (Seaside Ⅱ) of creeping bentgrass (*Agrostis stolonifera*) to high temperature stress to explore their different strategies. The plants were exposed to short-term high temperature

收稿日期: 2025-11-05; 改回日期: 2026-01-22
基金项目: 四川农业大学双支计划资助。
作者简介: 葛秋岑(2001－), 女, 四川泸州人, 在读硕士。E-mail: 1821473714@qq. com; 祁虹银(1996－), 男, 重庆人, 在读博士。E-mail: 843845085@qq. com。 ** 共同第一作者 These authors contributed equally to this work.
* 通信作者 Corresponding author. E-mail: lizhou1986814@163. com

stress at 38 ℃, and then the changes in lipid composition and soluble sugars content in leaves were determined. The results show that 3 hours of short-term high temperature stress did not cause significant changes in the fructose content in the leaves of the two cultivars, but significantly increased the sucrose content in 13M and the glucose content in Seaside Ⅱ. Lipidomics analysis showed that the contents of total lipids, phospholipids, glycolipids, and sphingolipids in heat-sensitive Seaside Ⅱ decreased significantly in response to short-term heat stress. In heat-resistant 13M, the total lipids and sphingolipids content remained unchanged in response to short-term heat stress, whereas the phospholipids content increased and the glycolipids content decreased significantly. Compared with heat-sensitive Seaside Ⅱ, heat-tolerant 13M accumulated larger amounts of total lipids, glycolipids (sulfoquinovosyl monoacylglycerol, monogalactosyl diacylglycerol, and monogalactosyl monoacylglycerol), phospholipids (phosphatidic acid, phosphatidylinositol phosphate, lysophosphatidylserine, lysophosphatidylinositol, lysophosphatidylglycerol, and mono-lysocardiolipin), and sphingolipids (dihexosyl N-acetylhexosyl ceramide, ceramide phosphate, dihexosyl ceramide, trihexosyl ceramide) in response to short-term high temperature stress. These changes indicate that 13M was able to maintain cell membrane integrity and stability under heat stress. In addition, 13M and Seaside Ⅱ showed different strategies in terms of the phospholipid signaling pathway in response to high temperature stress. In 13M, short-term heat stress resulted in the accumulation of phosphatidic acid, whereas in Seaside Ⅱ, it resulted in increased synthesis of phosphatidylinositol and phosphatidylinositol triphosphate. These results show that 13M and Seaside Ⅱ, which have different degrees of heat tolerance, have different lipid and glucose metabolic responses to short-term heat stress. The capacity of 13M to maintain higher contents of lipids and lipid signaling substances under heat stress may contribute to its heat tolerance. These results highlight a new concept for improving the heat tolerance of cold-season turfgrasses. However, whether the difference in heat tolerance between 13M and Seaside Ⅱ is solely related differences in lipid-sugar conversion under heat stress remains to be further studied.

Key words: *Agrostis stolonifera*; high temperature stress; lipid metabolism; sucrose; fructose; glucose

植物在生长发育过程中往往会受到各种非生物因子的胁迫,其中温度是影响植物生长发育的主要因子[1]。随着全球气候变暖,极端高温频发,热胁迫成了阻碍植物分布与健康生长的重要环境胁迫因素[2]。热胁迫也会对冷季型草坪草的生长和管理产生不利影响,使夏季草坪质量显著下降,草坪维护成本增加[3]。匍匐翦股颖(*Agrostis stolonifera*)是一种禾本科多年生冷季型草坪草,其质地柔软,耐低刈割,被广泛用于高尔夫球场、网球场及绿地景观草坪。然而,较差的耐热性限制了其在热带和亚热带地区的大面积推广应用[4]。以往的研究发现,高温引起匍匐翦股颖叶片衰老会导致草坪质量下降,高温诱导翦股颖叶片衰老的核心因素之一是活性氧(reactive oxygen species, ROS)过度积累导致膜脂过氧化[5]。因此,如何提高匍匐翦股颖的耐热性是草坪生产和养护管理过程中亟需解决的问题。

脂质不仅是生物膜的主要成分,还在能量转换、碳储备、信号转导以及胁迫应答等多方面发挥着不可估量的作用[6]。植物体内常见的脂类主要包括磷脂(phospholipids, Phls)、糖脂(glycolipids, Glls)和鞘脂(sphingolipids, Spls)。磷脂是形成细胞膜脂质双分子层的重要组成部分,也是高温胁迫下植物细胞中应激信号转导的次级信号分子[7]。已有研究表明,包括磷脂酰肌醇(phosphatidylinositol, PI)和磷脂酸(phosphatidic acid, PA)在内的各种信号脂质的产生在响应环境胁迫的植物中被放大,有助于调节下游信号通路并提高植物的非生物胁迫耐受性[8]。糖脂是在细胞膜稳定性和完整性中发挥重要功能的另一组重要脂质,其中双半乳糖基二酰基甘油(digalactosyl diacylglycerol, DGDG)和单半乳糖基二酰基甘油(monogalactosyl diacylglycerol, MGDG)是植物中两种丰富的类囊体脂质,有研究表明DGDG与MGDG含量的下降会导致植物叶绿素含量和光化学效率的下降[9]。鞘脂是一类复杂的脂质分子,其核心结构由鞘氨醇或其衍生物构成。它们是细胞膜的重要组成成分,不仅参与膜结构的形成,还在细胞信号传导、细胞识别、凋亡等生理过程中发挥关键作用。研究表明,鞘脂在番茄(*Solanum lycopersicum*)抗低温胁迫中发挥了积极作用[10]。然而,鞘脂含量及其组成在高温和低温等温度胁迫下的动态变

化与植物耐逆性之间的关系仍有待于深入研究。

糖类作为主要的光合同化物和信号分子，参与调控植物生长及其对各种非生物胁迫的响应，包括光合作用、碳分配、胚胎发育、种子萌发和叶片衰老等[11]。例如，果糖和葡萄糖在细胞分裂中发挥积极作用，而蔗糖则参与细胞分化和成熟过程[12]。在水稻（*Oryza sativa*）中，蔗糖是碳水化合物从光合活性组织（即源，主要是成熟叶）运输到非光合库如花药、雌蕊和种子的主要形式。籽粒灌浆过程中源库互作的破坏会导致结实性变差，籽粒变小。在源端，热胁迫降低了光系统 Ⅱ（photosystem Ⅱ，PS Ⅱ）的效率，以及二磷酸核酮糖羧化酶（ribose diphosphate carboxylase，Rubisco）和淀粉合成酶的活性，抑制了植物的能量代谢，也加剧了由于光呼吸导致的活性氧积累[13]。在长期的高温胁迫下，匍匐翦股颖可以通过提高蔗糖、果糖和葡萄糖的含量以增强细胞渗透调节能力，从而应对高温胁迫导致的水分失衡和细胞膜稳定性降低问题[14]。本研究以两种耐热型不同的匍匐翦股颖为对象，通过脂质组学分析探究了短期高温胁迫对叶片各类脂质及可溶性糖类含量变化的影响。研究结果将有助于了解短期高温胁迫下匍匐翦股颖的热响应策略，揭示不同匍匐翦股颖栽培品种间的耐热差异，为其更好地栽培管理提供理论依据。

1　材料与方法

1.1　供试材料与处理

试验地点为四川省成都市四川农业大学温江校区，试验采用耐热匍匐翦股颖品种 13M 和热敏感品种 Seaside Ⅱ。其中，Seaside Ⅱ是由 Tee 2 Green 公司在 1996 年育成的匍匐翦股颖品种，由于其优秀的耐盐性而受到广泛推广应用，但其耐热性较差，属于热敏感型品种。13M 则是由美国育成的耐热型匍匐翦股颖新品种[15]。试验开始于 2021 年春季，采用砂培的方法培育材料，种子播种量为 10 g·m^{-2}。石英砂中先倒入蒸馏水，待种子萌发 7 d 后将蒸馏水倒出，然后用 Hoagland 全营养液在光照培养箱中继续培养。培养箱温度设置为白天 23 ℃，夜晚 19 ℃，时长为各 12 h，相对湿度为 70%，光照强度为 650 μmol·m^{-2}·s^{-1}。当幼苗长至 30 d 时选取长势一致的材料进行高温胁迫处理 3 h，高温设置为 38 ℃，其他条件不变。试验共设置 4 个不同处理，每个处理 4 个独立重复（4 盆），4 个处理分别为：1）13M-C：生长 30 d 的 13M 正常条件下 3 h 后取样；2）13M-H：生长 30 d 的 13M 高温胁迫 3 h 后取样；3）S2-C：生长 30 d 的 Seaside Ⅱ正常条件下 3 h 后取样；4）S2-H：生长 30 d 的 Seaside Ⅱ高温胁迫 3 h 后取样。样品用于测定叶片可溶性糖类及脂质含量。

表 1　鉴定到的脂质种类及其简称

Table 1　The identified lipid classes and their abbreviations

名称 Name	英文缩写 English abbreviation
磺基奎诺糖基单酰基甘油 Sulfoquinovosyl monoacylglycerol	SQMG
磺基奎诺糖基二酰基甘油 Sulfoquinovosyl diacylglycerol	SQDG
单半乳糖基单酰基甘油 Monogalactosyl monoacylglycerol	MGMG
单半乳糖基二酰基甘油 Monogalactosyl diacylglycerol	MGDG
双半乳糖基单酰基甘油 Digalactosyl monoacylglycerol	DGMG
双半乳糖基二酰基甘油 Digalactosyl diacylglycerol	DGDG
磷脂酸 Phosphatidic acid	PA
磷脂酰丝氨酸 Phosphatidylserine	PS
磷脂酰甘油 Phosphatidylglycerol	PG
磷脂酰乙醇胺 Phosphatidylethanolamine	PE
卵磷脂 Phosphatidylcholine	PC
磷脂酰肌醇 Phosphatidylinositol	PI
磷脂酰肌醇磷酸酯 Phosphatidylinositol phosphate	PIP
磷脂酰肌醇二磷酸 Phosphatidylinositol diphosphate	PIP2
磷脂酰肌醇三磷酸 Phosphatidylinositol triphosphate	PIP3
溶血磷脂酰丝氨酸 Lyso phosphatidylserine	LPS
溶血磷脂酸 Lyso phosphatidic acid	LPA
溶血磷脂酰肌醇 Lyso phosphatidylinositol	LPI
溶血磷脂酰乙醇胺 Lyso phosphatidylethanolamine	LPE
溶血磷脂酰甘油 Lyso phosphatidylglycerol	LPG
溶血磷脂酰胆碱 Lyso phosphatidylcholine	LPC
心磷脂 Cardiolipin	CL
溶血素心磷脂 Di-lyso cardiolipin	DLCL
单溶血心磷脂 Mono-lyso cardiolipin	MLCL
神经酰胺 Ceramide	Cer
二己糖基 N-乙酰基己糖基神经酰胺 Dihexosyl N-acetylhexosyl ceramide	CerG2GNAc1
磷酸神经酰胺 Ceramide phosphate	CerP
己糖神经酰胺 Hexosyl ceramide	Hex1Cer
二己糖神经酰胺 Dihexosyl ceramide	Hex2Cer
三己糖神经酰胺 Trihexosyl ceramide	Hex3Cer

1.2 测定方法

1.2.1 糖含量测定　蔗糖、葡萄糖和果糖含量使用苏州格瑞斯生物科技有限公司试剂盒测定，其试剂盒货号为G0545W。

1.2.2 脂质组测定　先切取0.4 g新鲜叶片，放置于2 mL冻存管中，待测时使用冷冻干燥剂进行冻干处理。冻干后对样品打碎，取打碎后的叶片0.05 g加入300 μL的氯仿∶甲醇(2∶1)溶液，振荡混匀30 min。以12000 r·min^{-1}进行常温离心30 min，取150 μL上清液备用。将剩余沉淀物加入300 μL异丙醇溶液，同样进行30 min的振荡混匀后，12000 r·min^{-1}进行常温离心30 min，提取150 μL上清液与前上清液合并。最后，将上清液进行混匀后加入进样管中4 ℃保存，用于脂质组学分析[16]。表1为本次试验共鉴定出的脂质种类。

1.3 统计分析

使用Excel进行数据整理和统计，使用双因素方差分析比较不同处理间的差异显著性($P<0.05$)，最后采用Origin 2022进行图表绘制。

2 结果与分析

2.1 短期高温对匍匐翦股颖叶片糖分含量变化的影响

从图1A中可以观察到，正常条件下13M与Seaside Ⅱ叶片内果糖含量未有显著差异。高温胁迫下13M的果糖含量未受显著影响，而Seaside Ⅱ的果糖有所降低(图1A)。正常条件下Seaside Ⅱ叶片内的蔗糖含量显著高于13M，短期高温胁迫后，13M叶片内的蔗糖含量上升了11.68%(图1B)，但对Seaside Ⅱ叶片未产生显著影响(图1B)。正常条件下13M和Seaside Ⅱ叶片内葡萄糖含量没有显著差异(图1C)。与正常条件相比，热敏感型材料Seaside Ⅱ体内的葡萄糖含量上升了23.85%，显著高于13M(图1C)。

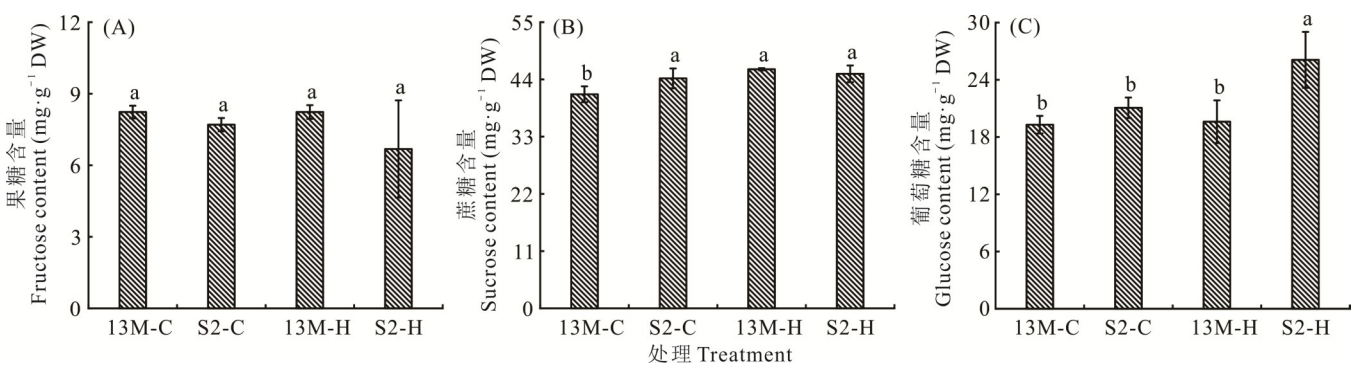


图1　短期高温对13M与Seaside Ⅱ叶片中果糖、蔗糖和葡萄糖含量的影响

Fig. 1　Effects of short-term high temperature on the contents of fructose, sucrose and glucose in leaves of 13M and Seaside Ⅱ

不同字母表示在0.05水平上差异显著($P<0.05$)。下同。DW为计算时的植物叶片干重。Different letters indicate significant difference at $P<0.05$ level. The same below. DW is the calculated dry weight of plant leaves.

2.2 短期高温对匍匐翦股颖叶片总脂质变化的影响

通过质谱分析，叶片脂质组分析共鉴定到30种脂质，其中包括6种糖脂、18种磷脂和6种鞘脂(表1)。正常条件下两个品种叶片内的总脂质相对含量没有显著差异(图2A)。在短期高温胁迫下，热敏感型材料Seaside Ⅱ叶片内的总脂质相对含量下降了13.31%，耐热型品种13M的总脂质相对含量未产生显著变化(图2A)。正常条件下Seaside Ⅱ叶片内的磷脂相对含量略高于13M，短时间的高温胁迫使13M中的磷脂相对含量显著上升了28.12%，而Seaside Ⅱ却降低了22.26%(图2B)。在正常条件和高温胁迫下，13M叶片内的糖脂相对含量均显著高于Seaside Ⅱ，高温胁迫3 h后13M和Seaside Ⅱ中的糖脂相对含量与他们各自正常条件下的糖脂相对含量相比没有发生显著变化(图2C)。在短期高温胁迫下，Seaside Ⅱ体内的鞘脂相对含量显著降低了18.62%，而13M的鞘脂相对含量没有发生显著变化(图2D)。短期高温胁迫后13M叶片内的鞘脂含量显著高于Seaside Ⅱ(图2D)。

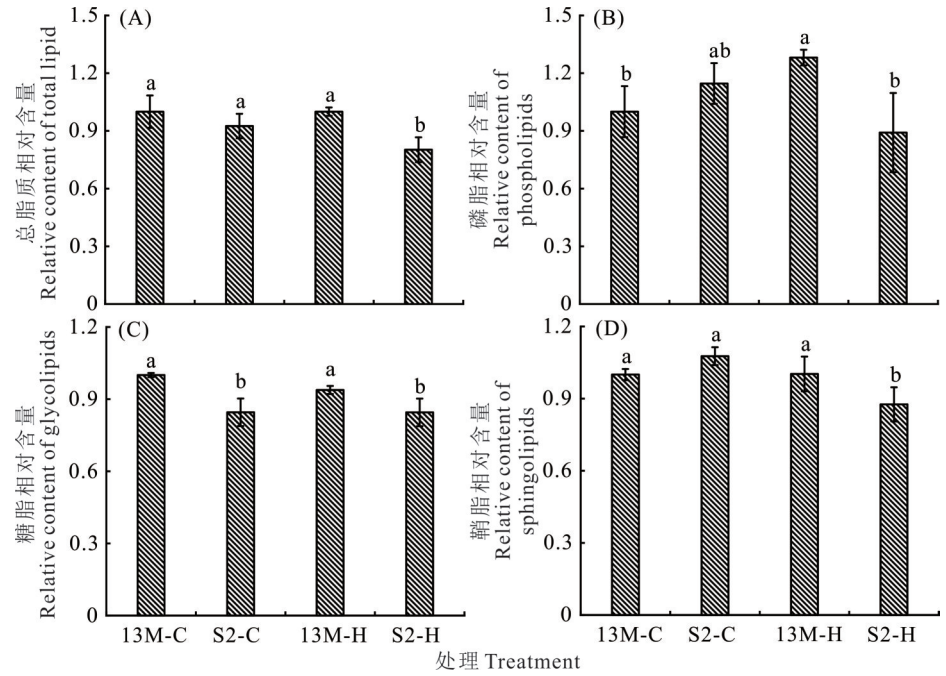


图 2　短期高温对 13M 与 Seaside Ⅱ 叶片中总脂质、磷脂、糖脂和鞘脂含量的影响

Fig. 2　Effects of short-term high temperature on the contents of total lipids, phospholipids, glycolipids, and sphingolipids in leaves of 13M and Seaside Ⅱ

2.3　短期高温对匍匐翦股颖叶片内糖脂含量的影响

正常条件下两个品种叶片内 SQMG 含量没有显著差异。高温处理 3 h 后，SQMG 在 13M 和 Seaside Ⅱ 中分别显著升高了 14.47% 和 9.98%（图 3A）。短期热胁迫没有对磺基奎诺糖基二酰基甘油（SQDG）的含量产生显著影响，正常和胁迫条件下两个品种叶片中的 SQDG 含量也没有显著差异（图 3B）。短期热胁迫后单半乳糖基单酰基甘油（MGMG）在 13M 和 Seasside Ⅱ 中分别升高了 170.73% 和 41.03%（图 3C）。虽然正常条件下 MGMG

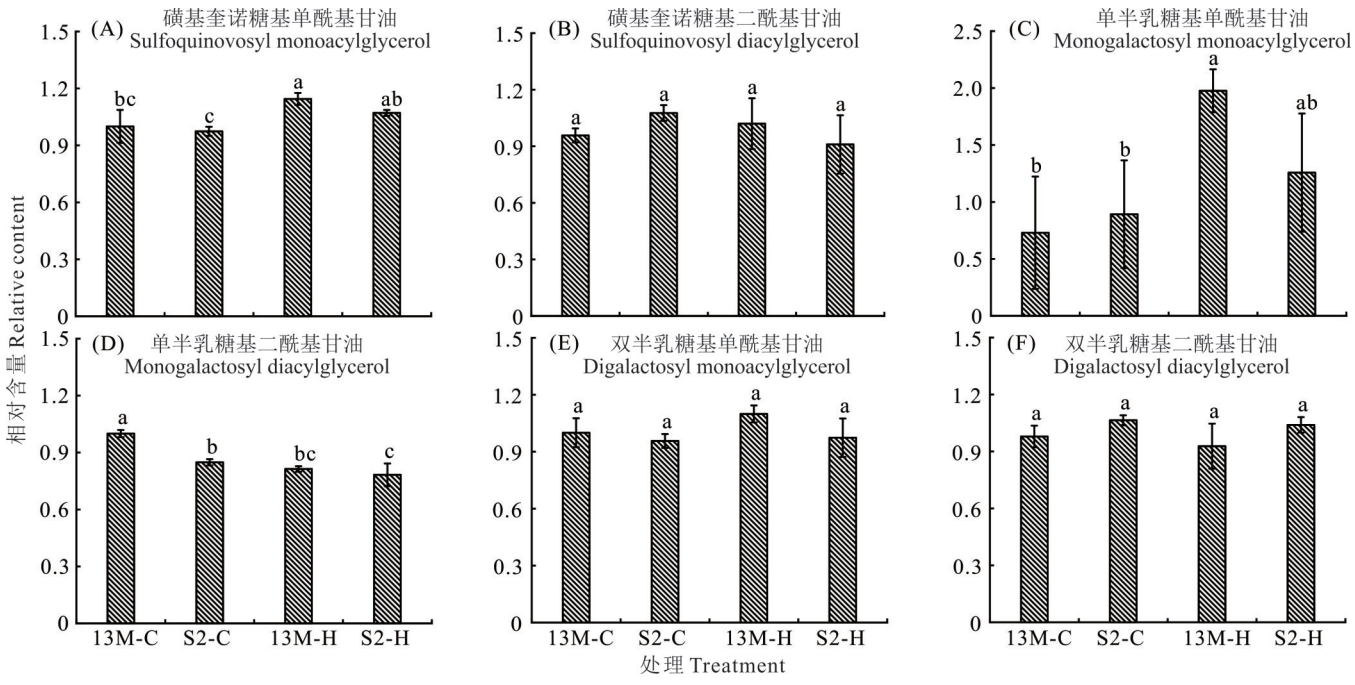


图 3　短期高温对 13M 与 Seaside Ⅱ 叶片中不同糖脂含量的影响

Fig. 3　Effects of short-term high temperature on the contents of different glycolipids in leaves of 13M and Seaside Ⅱ

的含量在两个品种中没有显著差异,但热胁迫下13M的MGMG含量更高(图3C)。正常条件下,耐热型材料13M中MGDG含量显著高于热敏感型材料Seaside Ⅱ;遭受短期高温胁迫后,耐热型材料13M中MGDG含量下降了18.65%,热敏感型材料SeasideⅡ下降了7.8%,此时二者之间的MGDG含量没有显著差异(图3D)。正常条件和短期高温胁迫下双半乳糖基单酰基甘油(DGMG)和DGDG在两个品种中没有显著差异(图3E和F)。

2.4 短期高温对匍匐翦股颖叶片内磷脂含量的影响

与未受到胁迫时相比,高温处理3 h后,13M中PA含量上升了65.39%,而Seaside Ⅱ下降了53.11%(图4A),Seaside Ⅱ中磷脂酰丝氨酸(PS)的含量下降了18.76%(图4B)。磷脂酰甘油(PG)的含量在4个处理中没有显著差异(图4C),但短期高温胁迫下13M中的PA和磷脂酰肌醇磷酸酯(PIP)含量显著高于Seaside Ⅱ(图4A和G)。高温胁迫3 h后,两个品种中磷脂酰肌醇二磷酸(PIP2)的含量均显著降低(图4H)。正常条件和高温胁迫下,Seaside Ⅱ具有较高的PIP3含量,且差异显著(图4I)。正常条件下Seaside Ⅱ中磷脂酰乙醇胺(PE)和卵磷脂(PC)的含量显著高于13M,高温胁迫下Seaside Ⅱ中PC和PI含量也显著高于13M(图4D~F)。此外,在遭受短期高温胁迫后,13M中的溶血磷脂酰丝氨酸(LPS)、溶血磷脂酰肌醇(LPI)、溶血磷脂酰甘油(LPG)、溶血素心磷脂(DLCL)、单溶血心磷脂(MLCL)含量显著高于Seaside Ⅱ,但溶血磷脂酸(LPA)、溶血磷脂酰乙醇胺(LPE)、溶血磷脂酰胆碱(LPC)、心磷脂(CL)的含量没有显著差异(图5)。Seaside Ⅱ中LPE含量在短期高温胁迫后下降了56.39%,13M中的LPE含量在胁迫前后没有发生显著变化(图5D)。高温胁迫还使13M与Seaside Ⅱ中的CL含量分别下降了21.79%和20.71%(图5G)。两种材料中的LPA与LPC含量在正常和高温条件下均没有发生显著变化(图5B和F)。

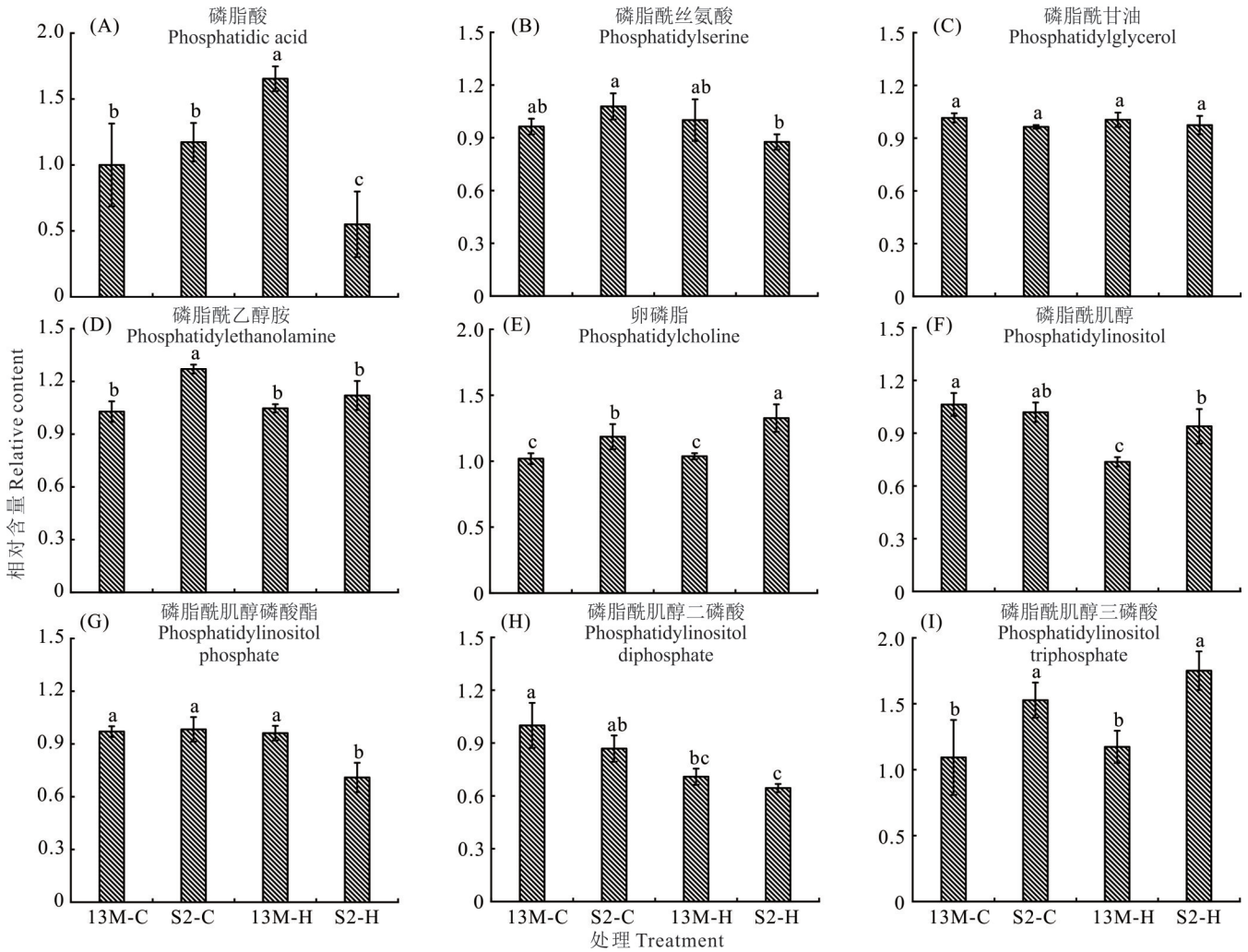


图4 短期高温对13M与Seaside Ⅱ叶片内不同常规磷脂含量的影响

Fig. 4 Effects of short-term high temperature on the contents of different common phospholipids in leaves of 13M and Seaside Ⅱ

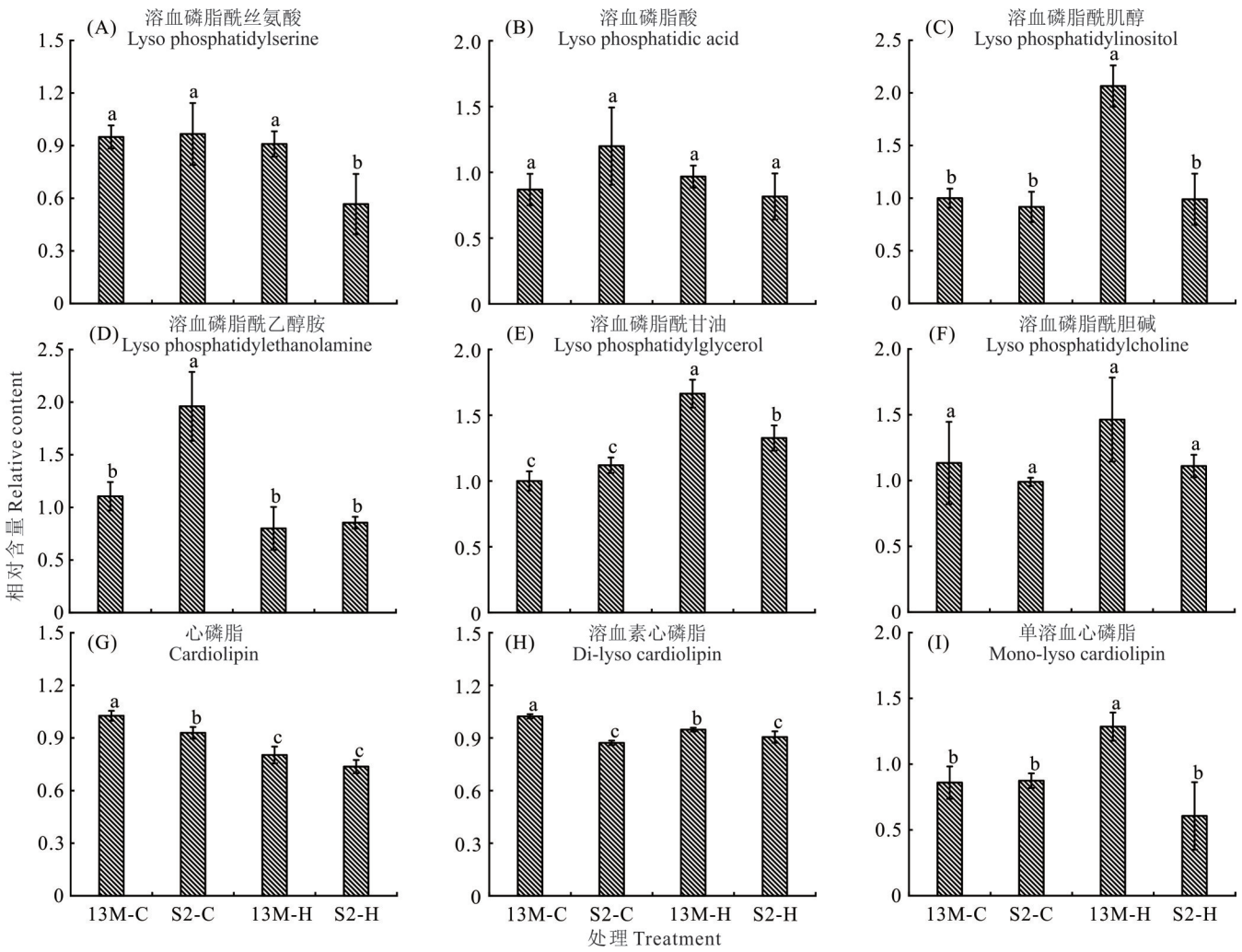


图 5　短期高温对 13M 与 Seaside Ⅱ叶片内不同溶血磷脂和心磷脂含量的影响

Fig. 5　Effects of short-term high temperature on the contents of different lysophospholipid and cardiolipin in leaves of 13M and Seaside Ⅱ

2.5　短期高温对匍匐翦股颖叶片内鞘脂含量的影响

本研究共检测到 6 种鞘脂。经过 3 h 的短期高温胁迫后，与正常条件相比，13M 中神经酰胺（Cer）含量显著升高，但 Seaside Ⅱ中神经酰胺（Cer）含量未发生显著变化（图 6A）。但值得注意的是，13M 中二己糖基 N-乙酰基己糖基神经酰胺（CerG2GNAc1）、磷酸神经酰胺（CerP）、二己糖神经酰胺（Hex2Cer）、三己糖神经酰胺（Hex3Cer）的含量在短期高温胁迫后均高于 Seaside Ⅱ（图 6B，C，E，F）。此外，Seaside Ⅱ中的己糖神经酰胺（Hex1Cer）含量与正常条件相比，下降了 19.8%，而 13M 的含量保持稳定（图 6D）。

3　讨论

脂质是生物膜的主要组成部分，而生物膜构成了细胞之间的界面，并将细胞划分为不同的隔室以利于生命活动[17]。先前的研究表明，非生物胁迫抑制了脂质的生物合成，表现为总脂质、磷脂、糖脂、鞘脂含量降低，例如干旱胁迫下的黑麦（*Secale cereale*）[18]，盐胁迫下的海滨雀稗（*Paspalum vaginatum*）[19]，热胁迫下的高羊茅（*Festuca arundinacea*）[20]和冷胁迫下的拟南芥（*Arabidopsis thaliana*）脂质含量下降[21]。此外，还有研究显示，干旱胁迫降低了两个白三叶（*Trifolium repens*）品种的总脂质、磷脂、鞘脂和糖脂含量，但抗旱型品种 Riverdel 的下降趋势小于干旱敏感型品种 Ladino[16]。本研究结果与其一致，耐热型 13M 在短期高温胁迫下总脂质相对含量没有发生显著变化，而热敏感型 Seaside Ⅱ的总脂质相对含量显著降低。此外，经过 3 h 短期高温胁迫后，13M 中的总脂质、磷

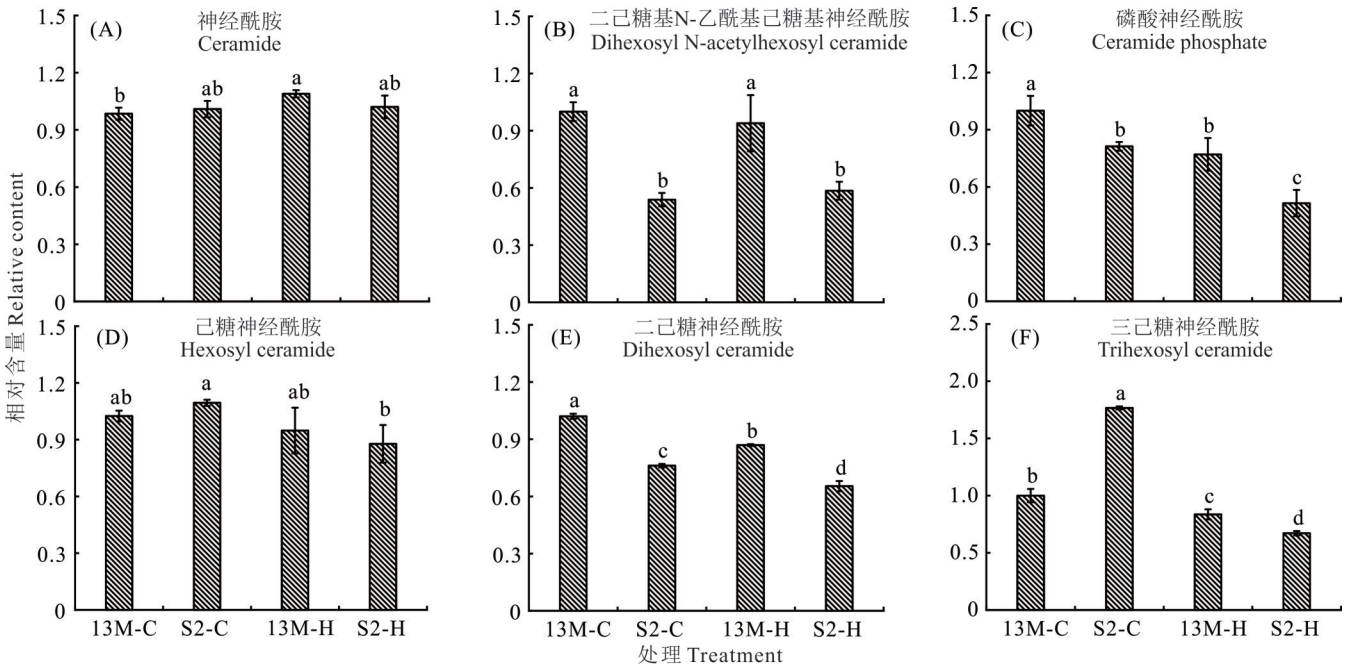


图6 短期高温对13M与Seaside Ⅱ叶片内不同鞘脂含量的影响

Fig. 6 Effects of short-term high temperature on the contents of different sphingolipids in leaves of 13M and Seaside II

脂、鞘脂含量比Seaside Ⅱ更高，这说明13M在高温条件下维持了较高的脂质代谢以抵御高温胁迫。糖脂DGDG、MGDG和SQDG是类囊体膜和叶绿体包膜的主要成分，在光合作用中起关键作用，其含量的降低会导致叶绿素降解和光合能力降低[7]。例如，耐热大豆(*Glycine max*)基因型在经历热胁迫后可以保持明显高于热敏基因型的DGDG和MGDG含量[22]。Lin等[23]研究发现，镉胁迫下耐镉品种Pixie可以保持比镉敏感品种Sulky更高的DGDG、DGMG、MGMG、SQDG和SQMG含量以及更高的DGDG/MGDG，这有助于胁迫下维持更好的叶绿体膜稳定性和完整性。本研究发现短期高温胁迫后耐热型品种13M中SQMG、MGMG、MGDG的含量比Seaside Ⅱ更高，这可能更利于13M在高温胁迫下保持类囊体膜的完整性和光合功能。

磷脂是形成细胞膜双分子层的重要组成成分，许多磷脂也是植物细胞中胁迫信号转导的次级信号分子[7]。PA是一种二酰基甘油磷脂，是许多复杂脂质生物合成的前体，并已被确定为细胞中最重要的第二信使[24]。PA信号产生主要依赖于两条途径：一是PC和PE等结构磷脂被磷脂酶D(phospholipase D, PLD)水解形成PA，二是依赖于磷脂酶C(phospholipase C, PLC)催化的水解反应和二酰甘油(diacylglycerol, DAG)磷酸化反应产生PA[25]。早期研究表明，PLD合成的PA参与了不同植物物种对低温胁迫[26]、热胁迫[27]的适应性响应。外施胺鲜脂(diethyl aminoethyl hexanoate, DA-6)改善白三叶的抗旱性与促进PA的合成有关，这有助于增强干旱胁迫下白三叶叶片细胞膜的稳定性、流动性和结构完整性[21]。还有研究表明，外源施用PA可显著提高冷季高羊茅的耐热性，并显著上调热休克途径[27]。在本试验中，匍匐翦股颖的两个品种在遭受短期高温胁迫后，13M体内的PA含量增加，而Seaside Ⅱ体内的PA含量减少，这表明13M可能通过PA信号通路激活热适应途径。PI是质膜的必需成分，参与维持逆境胁迫下细胞代谢活动的信号通路，PI也在各种磷脂的生物合成中起着关键的前体作用，例如合成PIP、PIP2和PA等信号磷脂[28]。研究发现，干旱锻炼能通过在整个热胁迫期间显著增加PI含量来提高冷季型草坪草高羊茅的耐热性[19]。通过上调PI的积累，耐热大豆基因型可以更好地适应热胁迫[22]。此外，PI快速转化为PIP，然后转化为PIP2，这个过程已被证明是植物对热胁迫的重要适应性反应之一[29]。本研究发现，3 h高温胁迫导致Seaside Ⅱ体内的PIP3含量显著升高，但这种现象在13M中未出现，这表明Seaside Ⅱ可能通过激活PIP3信号以应对高温胁迫，Seaside Ⅱ和13M在响应短期高温胁迫上存在差异。此外，在本研究中耐热型品种13M在热胁迫下积累的溶血磷脂含量(LPS、LPI、LPG、MLCL)也明显高于热敏型品种Seaside Ⅱ。越来越多的研究发现LPA、LPE和LPC等溶血磷脂在不同植物中起到调节信号传递、机械损伤应激响应、病原体感染信号传

递等功能[30-32]。然而,溶血磷脂在植物耐热性中的调节作用仍不清楚,值得进一步深入研究。

鞘脂既是脂质双分子层的结构成分,也参与不利环境条件下细胞内的信号转导[33]。例如,鞘脂的神经酰胺成分已被报道参与调节程序性细胞死亡(programmed cell death, PCD)[34]。鞘脂在脱落酸(abscisic acid, ABA)调节的保卫细胞关闭期间作为信号分子发挥至关重要的作用[35]。大多数鞘脂如Cer、Hex1Cer和CerG2GNAc1作为细胞膜的结构成分,其中一些还充当脂质信号分子,如Cer参与调节细胞代谢和更新[36],Cer含量的变化也影响植物内源激素水平和PCD[37]。CerG2GNAc1是动物体内的主要鞘脂基团,在植物中以微量存在,它们在植物中的潜在作用尚未得到很好的揭示[38-39]。Hex1Cer和Hex2Cer是质膜、植物细胞液泡膜和叶绿体膜包膜中高度丰富的鞘脂基团,参与维持膜的稳定性[40-41],Hex3Cer也是细胞膜双分子层中的主要鞘脂[42]。已有研究发现,在拟南芥低温胁迫期间,细胞膜中Hex1Cer的含量减少到1/2[20]。DA-6提高白三叶耐旱性与促进叶片中总鞘脂、Cer、Hex1Cer和CerG2GNAc1的积累有关[21]。耐镉白三叶品种在镉胁迫下能够积累更多的Cer、Cerp和Hex1Cer[23]。还有研究发现,与野生型相比,过表达*TrSAMDC1*的转基因拟南芥耐热性增强与热胁迫下提高叶片中Cer、Hex1Cer和CerG2GNAc1的水平有关[43]。与野生型相比,过表达*TrSAMDC1*的转基因拟南芥耐热性更强,也积累了更高的Her1Cer和Hex3Cer[44]。在本研究中,经过3 h的高温胁迫后,13M中的鞘脂含量(CerG2GNAc1、CerP、Hex2Cer、Hex3Cer)显著高于Seaside Ⅱ,这可能有助于热胁迫下13M维持更好的膜稳定性和信号转导途径。然而,这些鞘脂作为结构物质如何影响热胁迫下细胞膜的稳定性和流动性?这些鞘脂如何调节下游防御途径从而有助于提高植物的耐热性?这些问题仍需进一步研究和解决。

糖分作为能源物质、信号物质及渗透调节物质在植物应对非生物胁迫时发挥着重要作用[45]。Sharma等[46]研究发现,葡萄糖可以通过调控*HLP1*来增强拟南芥的抗热性。已有研究表明,高温胁迫显著影响了玉米(*Zea mays*)穗叶中淀粉和蔗糖代谢相关基因的表达和代谢物积累。在SYN5材料中,高温处理导致编码内切葡聚糖酶(endoglucanase, EGI)、ADP-葡萄糖焦磷酸化酶(ADP-glucose pyrophosphorylase, GLGC)、颗粒结合淀粉合成酶(granule-bound starch synthase, GBSS)和α-糖磷酸化酶(α-glucan phosphorylase, GP)的基因表达下调,而编码蔗糖合成酶(sucrose synthase, SUS)的基因表达上调。在JKN2000材料中,高温处理后仅EGI和β-葡萄糖苷酶(β-glucosidase, BGIB)的基因表达下调。同时,高温处理导致SYN5中葡萄糖1-磷酸(glucose 1-phosphat, G1P)含量降低,而JKN2000中葡萄糖6-磷酸(glucose 6-phosphat, G6P)含量增加。这些变化表明高温胁迫扰乱了淀粉和蔗糖的正常代谢途径,可能影响植物的能量供应和应激反应[47]。与耐热性弱的品种PENNEAGLE相比,高温胁迫下耐热性强的匍匐翦股颖品种PROVIDENCE积累了更多的果糖和来苏糖[48]。外施DA-6或γ-氨基丁酸(γ-aminobutyric acid, GABA)显著提高匍匐翦股颖耐热性与提高叶片蔗糖、果糖和葡萄糖的含量有关[49-50]。本试验结果发现,在短期高温胁迫下Seaside Ⅱ体内的葡萄糖含量和13M体内的蔗糖含量有所增加,表明高温胁迫早期匍匐翦股颖便开始通过促进糖分的积累以提高能量代谢及渗透调节能力来响应高温胁迫。此外,逆境胁迫下脂质会转化为糖以提高植物的抗逆性。细胞内甘油三酯(triacylglycerol, TAG)代谢参与储存能量的转换以及细胞内脂质稳态的维持,TAG被脂肪酶水解以产生脂肪酸和甘油,用于随后的糖异生,这为种子萌发和幼苗生长提供能量和碳骨架[51-52]。研究显示,糖依赖性蛋白(sugar-dependent protein, SDP6)催化甘油水解,*SDP6*基因缺失损害了拟南芥*sdp6*突变体中甘油向可溶性糖的转化,最终导致幼苗发育停滞[53]。大豆可以通过外源施用DA-6诱导脂质转化为糖,从而显著缓解其幼苗衰老[54]。重金属镉胁迫下,白三叶幼苗通过促进脂质向糖的转化从而有利于提高自身的耐镉性并改善胁迫下早期幼苗的生长[23]。这些研究表明脂质—糖转化途径通过维持能量供应在植株生长和抗逆性上发挥重要作用。然而在本研究中13M和Seaside Ⅱ的耐热性差异是否与促进脂—糖转化有关还有待进一步验证。

4　结论

综上所述,匍匐翦股颖耐热型品种13M在短期高温胁迫下比热敏感品种Seaside Ⅱ积累了更多总脂质、糖脂(SQMG、MGDG、MGMG)、磷脂(PA、PIP、LPS、LPI、LPG、MLCL)和鞘脂(CerG2GNAc1、CerP、Hex2Cer、Hex3Cer),这有利于热胁迫下13M保持较好的细胞膜完整性与稳定性,维持了细胞的正常功能。在磷脂信号通

路中13M与Seaside Ⅱ表现出了不同的高温响应策略,13M主要通过促进PA的积累,而Seaside Ⅱ则主要通过提高PI和PIP3的合成以响应热胁迫。此外,13M提高了蔗糖的积累而Seaside Ⅱ增加了葡萄糖的积累以响应短期热胁迫。然而,鞘脂在提高植物耐热性上的重要性以及13M和Seaside Ⅱ的耐热性差异是否与促进脂—糖转化有关仍需待进一步深入研究。

参考文献 References:

[1] Tu X J, Wang Q M, Rao L Q. Effects of high temperature stress on physiology and biochemistry of plant. Hunan Agricultural Science, 2013, 43(13): 28—30.
屠小菊, 汪启明, 饶力群. 高温胁迫对植物生理生化的影响. 湖南农业科学, 2013, 43(13): 28—30.

[2] Xie Y L. Research progress on the effects of high temperature stress on plant physiology. Jilin Agriculture, 2019, 19(8): 107—108.
解玉玲. 高温胁迫对植物生理影响的研究进展. 吉林农业, 2019, 19(8): 107—108.

[3] Huang C, Tian Y L, Zhang B B, *et al*. Chitosan (CTS) alleviates heat-induced leaf senescence in creeping bentgrass by regulating chlorophyll metabolism, antioxidant defense, and the heat shock pathway. Molecules, 2021, 26(17): 5337.

[4] Zeng W, Hassan M J, Kang D, *et al*. Photosynthetic maintenance and heat shock protein accumulation relating to γ-aminobutyric acid (GABA)-regulated heat tolerance in creeping bentgrass. South African Journal of Botany, 2021, 141(6): 405—413.

[5] Li Z, Zeng W H, Cheng B Z, *et al*. Turf quality and physiological responses to summer stress in four creeping bentgrass cultivars in a subtropical zone. Plants, 2022, 11(5): 665.

[6] Yao N. Advances in plant lipid biology. Plant Physiology Journal, 2018, 54(12): 1747.
姚楠. 植物脂质生物学进展. 植物生理学报, 2018, 54(12): 1747.

[7] Higashi Y, Saito K. Lipidomic studies of membrane glycerolipids in plant leaves under heat stress. Progress in Lipid Research, 2019, 75(3): 100990.

[8] Cowan A K. Phospholipids as plant growth regulators. Plant Growth Regulation, 2006, 48(2): 97—109.

[9] Chen J P, Burke J J, Xin Z G, *et al*. Characterization of the *Arabidopsis* thermosensitive mutant *atts02* reveals an important role for galactolipids in thermotolerance. Plant Cell & Environment, 2006, 29(7): 1437—1448.

[10] Zhou Y, Zeng L T, Fu X M, *et al*. The sphingolipid biosynthetic enzyme *Sphingolipid delta8 desaturase* is important for chilling resistance of tomato. Scientific Reports, 2016, 6(1): 38742.

[11] Asad M A U, Yan Z, Zhou L, *et al*. How abiotic stresses trigger sugar signaling to modulate leaf senescence? Plant Physiology and Biochemistry, 2024, 210(5): 108650.

[12] Lembrechts R, Ceusters N, Dd Proft M P, *et al*. Sugar and starch dynamics in the medium-root-leaf system indicate possibilities to optimize plant tissue culture. Scientia Horticulturae, 2017, 224(11): 226—231.

[13] Kumar S, Thakur M, Mitra R, *et al*. Sugar metabolism during pre- and post-fertilization events in plants under high temperature stress. Plant Cell Reports, 2021, 41(3): 655—673.

[14] Li Z, Yu J J, Peng Y, *et al*. Metabolic pathways regulated by abscisic acid, salicylic acid and γ-aminobutyric acid in association with improved drought tolerance in creeping bentgrass. Physiologia Plantarum, 2017, 159(1): 42.

[15] Li Z, Li Z, Tang M Y, *et al*. Adaptability to high temperature and stay-green genotypes associated with variations in antioxidant, chlorophyll metabolism, and γ-aminobutyric acid accumulation in creeping bentgrass species. Frontiers in Plant Science, 2021, 12(1): 750728.

[16] Hassan M J, Qi H Y, Cheng B Z, *et al*. Enhanced adaptability to limited water supply regulated by diethyl aminoethyl hexanoate (DA-6) associated with lipidomic reprogramming in two white clover genotypes. Frontiers in Plant Science, 2022, 13(1): 879331.

[17] Hou Q, Ufer G, Bartels D. Lipid signalling in plant responses to abiotic stress. Plant, Cell & Environment, 2016, 39(5): 1029—1048.

[18] Dawid P, Sylwia K, Aneta S, *et al*. Remodeling of leaf cellular glycerolipid composition under drought and re-hydration conditions in grasses from the *Lolium-Festuca* complex. Frontiers in Plant Science, 2016, 7(1): 01027.

[19] Gao Y L, Li M N, Zhang X X, *et al*. Up-regulation of lipid metabolism and glycine betaine synthesis are associated with choline-induced salt tolerance in halophytic seashore paspalum. Plant, Cell & Environment, 2020, 43(1): 159—173.

[20] Zhang X X, Xu Y, Huang B R. Lipidomic reprogramming associated with drought stress priming-enhanced heat tolerance in tall

fescue (*Festuca arundinacea*). Plant, Cell & Environment, 2019, 42(3): 947－958.

[21] Nagano M, Ishikawa T, Ogama Y, *et al*. *Arabidopsis* Bax inhibitor-1 promotes sphingolipid synthesis during cold stress by interacting with ceramide-modifying enzymes. Planta, 2014, 240(1): 77－89.

[22] Narayanan S, Zoong-lwe Z S, Gandhi N, *et al*. Comparative lipidomic analysis reveals heat stress responses of two soybean genotypes differing in temperature sensitivity. Plants, 2020, 9(4): 457.

[23] Lin L, Lin J N, Zhou M, *et al*. Lipid remodelling and the conversion of lipids into sugars associated with tolerance to cadmium toxicity during white clover seed germination. Physiologia Plantarum, 2024, 176(4): e14433.

[24] Testerink C, Munnik T. Phosphatidic acid: a multifunctional stress signaling lipid in plants. Trends in Plant Science, 2005, 10(8): 368－375.

[25] Heilmann I. Phosphoinositide signaling in plant development. Development, 2016, 143(12): 2044－2055.

[26] Li W Q, Li M Y, Zhang W H, *et al*. The plasma membrane-bound phospholipase Dδ enhances freezing tolerance in *Arabidopsis thaliana*. Nature Biotechnology, 2004, 22(4): 427－433.

[27] Wang X Y, Huang B R. Lipid- and calcium-signaling regulation of *HsfA2c*-mediated heat tolerance in tall fescue. Environmental & Experimental Botany, 2017, 136(4): 59－67.

[28] Xue H W, Chen X, Mei Y. Function and regulation of phospholipid signalling in plants. Biochemical Journal, 2009, 421(2): 145－156.

[29] Liu Y N, Lu X X, Ren A, *et al*. Conversion of phosphatidylinositol (PI) to PI4-phosphate (PI4P) and then to PI (4, 5) P2 is essential for the cytosolic Ca^{2+} concentration under heat stress in *Ganoderma lucidum*. Environmental Microbiology, 2018, 20(7): 2456－2468.

[30] Lee S, Suh S, Kim S, *et al*. Systemic elevation of phosphatidic acid and lysophospholipid levels in wounded plants. The Plant Journal, 1997, 12(3): 547－556.

[31] Wi S J, Seo S Y, Cho K, *et al*. Lysophosphatidylcholine enhances susceptibility in signaling pathway against pathogen infection through biphasic production of reactive oxygen species and ethylene in tobacco plants. Phytochemistry, 2014, 104(8): 48－59.

[32] Lee B H, Choi S H, Kim H J, *et al*. Plant lysophosphatidic acids: A rich source for bioactive lysophosphatidic acids and their pharmacological applications. Biologic and Pharmaceutical, 2016, 39(2): 156－162.

[33] Michaelson L V, Napier J A, Molino D, *et al*. Plant sphingolipids: Their importance in cellular organization and adaption. Biochimica et Biophysica Acta (BBA)－Molecular and Cell Biology of Lipids, 2016, 1861(9): 1329－1335.

[34] Liang H, Yao N, Song J T, *et al*. Ceramides modulate programmed cell death in plants. Genes & Development, 2003, 17(21): 2636－2641.

[35] Coursol S, Fan L M, Stunff H L, *et al*. Sphingolipid signalling in *Arabidopsis* guard cells involves heterotrimeric G proteins. Nature, 2003, 423(6940): 651－654.

[36] Pineau B, Bourge M, Marion J, *et al*. The importance of cardiolipin synthase for mitochondrial ultrastructure, respiratory function, plant development, and stress responses in *Arabidopsis*. The Plant Cell, 2013, 25(10): 4195－4208.

[37] Berkey R, Bendigeri D, Xiao S Y. Sphingolipids and plant defense/disease: the "death" connection and beyond. Frontiers in Plant Science, 2012, 3(1): 68.

[38] Lester R L, Dickson R C. Sphingolipids with inositolphosphate-containing head groups. Advances in Lipid Research, 1993, 26(1): 253－274.

[39] Tafesse F G, Ternes P, Holthuis J C M. The multigenic sphingomyelin synthase family. Journal of Biological Chemistry, 2006, 281(40): 29421－29425.

[40] Lynch D V, Steponkus P L. Plasma membrane lipid alterations associated with cold acclimation of winter rye seedlings (*Secale cereale*). Plant Physiology, 1987, 83(4): 761－767.

[41] Uemura M, Steponkus P L. A contrast of the plasma membrane lipid composition of oat and rye leaves in relation to freezing tolerance. Plant Physiology, 1994, 104(2): 479－496.

[42] Sperling P, Heinz E. Plant sphingolipids: structural diversity, biosynthesis, first genes and functions. Biochimica et Biophysica Acta (BBA)－Molecular and Cell Biology of Lipids, 2003, 1632(1/2/3): 1－15.

[43] Li Z, Cheng B Z, Zhao Y, *et al*. Metabolic regulation and lipidomic remodeling in relation to spermidine-induced stress tolerance to high temperature in plants. International Journal of Molecular Sciences, 2022, 23(20): 12247.

[44] Cheng B Z, Zhou M, Tang T, *et al*. A *Trifolium repens flavodoxin-like quinone reductase 1* (*TrFQR1*) improves plant adaptability to high temperature associated with oxidative homeostasis and lipids remodeling. The Plant Journal, 2023, 115(2):

369－385.

[**45**] Liu Y H, Offler C E, Ruan Y L. Regulation of fruit and seed response to heat and drought by sugars as nutrients and signals. Frontiers in Plant Science, 2013, 4(1): 282.

[**46**] Sharma M, Banday Z Z, Shukla B N, *et al*. Glucose-regulated *HLP1* acts as a key molecule in governing thermomemory. Plant Physiology, 2019, 180(2): 1081－1100.

[**47**] Wang Z T, Guo J, Luo W X, *et al*. Salicylic acid cooperates with lignin and sucrose signals to alleviate waxy maize leaf senescence under heat stress. Plant, Cell & Environment, 2025, 48(6): 4341－4355.

[**48**] Du Y, Zhao Y, Li Z. Different heat tolerance of two creeping bentgrass cultivars related to altered accumulation of organic metabolites. Agronomy, 2025, 15(7): 1544.

[**49**] Li Z, Zhou M, Qi H Y, *et al*. Foliar application of diethyl aminoethyl hexanoate (DA-6) alleviated summer bentgrass decline and heat damage to creeping bentgrass. Crop Science, 2024, 64(2): 1039－1050.

[**50**] Li Z, Yu J J, Peng Y, *et al*. Metabolic pathways regulated by γ-aminobutyric acid (GABA) contributing to heat tolerance in creeping bentgrass (*Agrostis stolonifera*). Scientific Reports, 2016, 6(1): 30338.

[**51**] Huang S X, Liu Z Q, Cao W H, *et al*. The plant ESCRT component FREE1 regulates peroxisome-mediated turnover of lipid droplets in germinating *Arabidopsis* seedlings. The Plant Cell, 2022, 34(11): 4255－4273.

[**52**] Aznar-moreno J A, Mukherjee T, Morley S A, *et al*. Suppression of *SDP1* improves soybean seed composition by increasing oil and reducing undigestible oligosaccharides. Frontiers in Plant Science, 2022, 13(1): 863254.

[**53**] Quettier A L, Shaw E, Eastmond P J. *SUGAR-DEPENDENT6* encodes a mitochondrial flavin adenine dinucleotide-dependent glycerol-3-P dehydrogenase, which is required for glycerol catabolism and postgerminative seedling growth in *Arabidopsis*. Plant Physiology, 2008, 148(1): 519－528.

[**54**] Zhou W G, Chen F, Zhao S H, *et al*. DA-6 promotes germination and seedling establishment from aged soybean seeds by mediating fatty acid metabolism and glycometabolism. Journal of Experimental Botany, 2019, 70(1): 101－114.