小麦茎鞘非结构性碳水化合物代谢与调控研究进展

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摘要 小麦遭遇逆境时花后光合作用减弱,茎鞘非结构性碳水化合物(NSC)作为主要灌浆物质来源对产量贡献率可达20%~50%。因此,了解茎鞘NSC的代谢规律,明确栽培管理措施和遗传育种改良对NSC代谢的影响,对于充分发挥NSC在小麦抗逆稳产中的作用具有重要意义。以小麦茎鞘NSC主要成分——果聚糖为例,概述了NSC的结构与合成、运输与降解;分析了小麦茎鞘NSC的功能,特别是对低温冻害和高温干旱逆境的响应;讨论了品种选择、水分管理、氮肥运筹等栽培措施对茎鞘NSC的调控作用;展望利用茎鞘NSC进行抗逆育种的前景。

关键词 非生物胁迫;抗逆性;产量;栽培措施;遗传改良

籽粒灌浆物质来源于花后光合物质生产和花前非结构性碳水化合物(NSC)转运[1-2]。20世纪第一次绿色革命,伴随着灌水和化肥的大量投入,特别是半矮秆品种的推广使得小麦等作物产量得到大幅提升,对收获指数提高起到了至关重要的作用[3]。首先,植株矮化使茎鞘发育对碳水化合物的需求减少,穗的同化物分配增加,增加了穗粒数;其次,叶片功能期延长,花后光合作用增强,增加了籽粒灌浆的“源”[4]。然而,大量开采地下水和过量施用化肥带来一系列生态环境问题,同时气候逐渐变暖,非生物逆境胁迫不断加剧。新的绿色革命迫切要求小麦持续稳定增产,但却面临缺水[5]、高温[6]、盐碱[7]、寡照[8]等诸多挑战。如何在较低水肥投入条件下实现小麦抗逆增产,成为小麦栽培学家和育种家的重要研究课题之一。

小麦的茎鞘不仅作为同化物运输器官,而且作为同化物临时储藏器官参与了植株源库关系的调节。小麦茎鞘NSC约占茎鞘总干重的40%以上[9],是籽粒产量的重要物质来源。小麦茎鞘NSC积累于拔节到灌浆期初期[10-11],之后向籽粒中转运[12]。作为临时储藏物,茎鞘NSC为产量形成持续提供同化物,贡献率在20%左右[13]。在逆境条件下,小麦叶片光合减弱同化物输出受阻,茎鞘NSC将成为籽粒主要同化物来源,其贡献率可达到50%以上[14]。此外,茎鞘NSC能够激发库活性促进籽粒灌浆强度。Slewinski[15]也指出调控茎鞘NSC将成为21世纪作物抗逆增产的重要途径。基于此,本文综述茎鞘NSC的代谢途径(以果聚糖为例),分析茎鞘NSC的功能,讨论小麦茎鞘NSC在抗逆稳产中的应用。

1 小麦茎鞘NSC的代谢途径

与纤维素和木质素等结构性物质主要参与形态建成不同,小麦茎鞘NSC是参与生命代谢的重要物质,主要包括果聚糖、蔗糖、葡萄糖和果糖。其中果聚糖是小麦茎鞘NSC主要的储藏形式,最高可达茎鞘NSC的85%;蔗糖是碳水化合物运输的主要形式,占茎鞘NSC的10%[11,16-17]。淀粉存在于小麦叶片和茎鞘中,其主要功能是为营养生长提供物质来源而不是转运到籽粒当中。本文主要以果聚糖为例概述茎鞘NSC的代谢途径。

1.1 果聚糖的结构与合成

Vijn等[18]将自然界中的果聚糖分为5类:线性菊糖型果聚糖(Inulin)、梯牧草糖型果聚糖(Levan)、混合型果聚糖(Branched)、菊糖型果聚糖新生系列(Inulin neoseries)和梯牧草糖型果聚糖新生系列(Levan neoseries)。小麦是混合型果聚糖(Branched)形式存在的典型代表[19],即以6-蔗果三糖为起始三糖,通过β(2-1)和β(2-6)2个糖苷键连接而成的混合类型。Bancal等[19]进一步指出,小麦茎鞘中的果聚糖主要是梯牧草糖型多聚体,以6-蔗果三糖为起始三糖,即只通过β

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(2-6)糖苷键连接而成的线性类型。

植物体内果聚糖的合成以蔗糖为中间体在薄壁细胞的液泡中进行[20]，根据Vijn等[18]建立的合成模型，包括2个合成酶，蔗糖：蔗糖1-果糖基转移酶(1-SST)和果聚糖：果聚糖1-果糖基转移酶(1-FFT)。一个蔗糖分子通过1-SST作用将果糖基转移到另一个蔗糖分子上，形成1个1-蔗果三糖并释放一个葡萄糖。该反应中，SST以蔗糖为专一受体，合成聚合度为3的果聚糖，主要催化果聚糖合成的第一步反应，也是控制碳素向果聚糖库分配的关键。随后1-FFT催化加链反应，聚合三糖或者寡聚糖产生更长聚合度的多糖。茎鞘注射^{14}C标记的蔗糖后果聚糖迅速被标记，表明小麦果聚糖的合成依赖蔗糖。据Duchateau等[21]报道，在小麦和大麦中，果聚糖：果聚糖6G-果糖基转移酶(6-SFT)也参与了果聚糖合成过程，由2个1-蔗果三糖产生6-蔗果三糖和1个新1-蔗果三糖。与1-FFT通过β(2-1)糖苷键进行加链不同，6-SFT可以连续地通过β(2-6)糖苷键进行加链[22]，进而形成梯牧草糖型(Levan)和混合型(Branched)果聚糖。然而，Goggin等[23]研究发现，小麦果聚糖的合成与FFT并不直接相关。果聚糖的糖链长度和分支结构与组织器官、遗传品种和所处环境关系密切，且果聚糖浓度通常与更高级的结构有关[24]。

1.2 果聚糖的运输与降解

茎鞘NSC以聚合物的形式存在于薄壁细胞中[17]，例如，果聚糖合成后主要存在于环绕在节间组织维管束周围的薄壁细胞中[25]，与薄壁细胞具有很好的共质连接性。通过这种共质区隔化，降低了碳水化合物的渗透压，从而使植物能在单位体积内储藏更多的碳水化合物[26]。

当茎鞘NSC转运时，果聚糖由果聚糖外切水解酶(FEH)催化降解。植物中的FEH有不同的类型，包括水解β(2-1)糖苷键的1-FEH[27]和水解β(2-6)糖苷键的6-FEH[28-29]，以及能水解两种糖苷键的水解酶[30]；近来，第3种水解酶1-FEHw3已经从小麦中得到纯化[31]。FEH的活性与细胞壁活性有关[32]，并受到蔗糖底物的反馈抑制[33]。在该酶作用下，果聚糖于液泡中由果糖基末端降解掉一个果糖残基，后被运出液泡，在细胞质中一次降解一个果糖残基，最终被降解为蔗糖。果聚糖最终以蔗糖的形式通过质外体途径被运输到韧皮部[34]，然后通过质外体和共质体两种途径进入籽粒库细胞。蔗糖最终通过转化酶(INV)和蔗糖合成酶(SS)被分解利用。转化酶(INV)催化蔗糖水解生成果糖和葡萄糖，是不可逆酶[35]；蔗糖合成酶(SS)是存在于细胞质中的可溶性酶，既可催化蔗糖合成又可催化蔗糖分解(果糖+UDPG$\longleftrightarrow$蔗糖+UDP)，但在茎鞘中主要起分解蔗糖的作用[36]。

2 小麦茎鞘NSC在抗逆稳产中的作用

理论上，茎鞘存储NSC的薄壁细胞与根和种子等终端库器官存在竞争关系[37]。当植物库强度很小时才将过量的碳水化合物以NSC的形式储藏在茎鞘中[38]，例如小麦茎鞘中的NSC只有在灌浆前期积累，灌浆后期则向籽粒当中转运[10-11]。植物体内过量的碳水化合物以NSC的形式储藏在茎鞘中，在不同时期和环境中对调节源库关系起重要作用[11]。与叶片相比，茎鞘NSC呼吸消耗少，需要能量小，因此，茎鞘NSC储存和转运代谢效率较高[17]。大量研究表明，小麦茎鞘NSC对于适应逆境并保持产量稳定性具有重要作用，例如低温冻害、花后干旱和花后高温等。

2.1 低温冻害

气候变暖特别是冬前温度升高容易引起冬小麦旺长，进而容易导致冬前冻害或早春倒春寒。代立芹等[39]指出气候变暖致使冬小麦冬前旺长现象突出，抗寒力下降，冻害风险较大，如2004—2005年黄淮海麦区、2005—2006年河北中南部麦区大面积冻害。

1964年，Trunova[40]发现在经历-3℃冻害数天后，小麦茎鞘果聚糖浓度降低并伴随单糖浓度的升高，表明小麦NSC含量或许与抗寒性存在一定相关性。Suzuki等[41]研究表明，与较低聚合度的果聚糖相比，小麦所含高聚合的果聚糖与抗寒性具有更密切的关系。Yukawa等[42]进一步研究表明，小麦茎鞘果聚糖含量与其抗寒性显著正相关。关于小麦所含果聚糖适应低温的原因，前人做了大量研究。Johannson等[43]指出果聚糖解聚释放大量游离果糖可降低组织水分的冰点，尽管降低程度很小，但这是抗低温的综合表现之一。另外，这也与果聚糖较高的水溶性、严寒下对膜的保护作用以及低温下正常的合成能力密切相关[18,42]。

2.2 花后干旱

华北地区是中国小麦主产区，但其70%的降雨集中在6—9月[44]，小麦生育期内120 mm左右的降雨远达不到其400—500 mm的水分需求[45]，特别是小麦籽粒灌浆期缺水严重，花后干旱成为限制产量形成的关键因素[46]。

与抗寒机制相似，干旱条件下植物能产生糖、胺类、多元醇等物质，使细胞免受渗透胁迫而对其起到保护作用[47]。在干旱导致植物组织细胞失水从而引起渗透胁迫时，果聚糖与淀粉相比具有可溶性，因此在细胞受到渗透胁迫时可以起到缓冲溶质的作用[23]。Veryken等[48]报道果聚糖可以插入磷脂囊泡的首基中，因此可以稳定细胞膜结构从而适应干旱胁迫。此外，花后干旱光合作用下降、同化物积累减少、灌浆持续期缩短，籽粒灌浆物质供应不足；但是，干旱促进了茎鞘NSC向籽粒转运，成为籽粒灌浆物质的主要来源，提高了灌浆强度，茎鞘NSC对产量的贡献率明显增加[49]。因此，在干旱条件下，具有较高茎鞘NSC的小麦品种往往具有较高的可育小花数、灌浆强度和稳定的产量[13]。Gupta等[50]研究发现，干旱条件下抗旱品种的茎鞘转运率高，蔗糖合成酶的活性较高，通过库积累物的卸载促进库的强度，进而增加了同化物向籽粒的转运。干旱品种因为茎鞘NSC转运延长了花后生育期，稳定了干旱条件下的产量。由此可知，抗旱品种可能是通过增加果聚糖贮存、提高转运率、提高库活性、延长灌浆

时间来稳定产量。

2.3 花后高温

随着气候变化,全球范围内温度升高已成为不争的事实,据IPCC预测21世纪末温度将升高1.8~5.8℃[51]。小麦对高温非常敏感,主产区小麦生育期内普遍存在温度升高的趋势[52]。小麦生育后期长时间或暂时性高温胁迫在未来为增加的趋势[53],尤其在籽粒灌浆期,高温直接影响小麦籽粒数和籽粒重,因而对小麦生产造成更为不利的影响[54]。

花后高温缩短了籽粒灌浆持续期,Streck等[55]报道每超过籽粒灌浆最适温度(15~25℃)1℃,小麦籽粒灌浆期减少2.8 d。Yin等[56]研究发现超过最适温度5℃时灌浆期减少了12 d,但籽粒灌浆速率增强。然而,灌浆速率的增加并不能补偿因灌浆持续期减少所造成的产量损失,尤其是在超过30℃时[57]。甚至有学者指出对一些粒重不稳定的品种而言,高温能同时缩短灌浆持续期并降低灌浆速率[58]。研究发现,当温度超过30℃时,旗叶向籽粒的同化物供应极大降低,但在1~50℃内茎鞘NSC向籽粒的同化物供应不受影响[59]。这表明,热胁迫对同化物运输的影响是间接的,尽管其降低了营养器官的同化物供应速率[60]。虽然高温诱导茎鞘NSC转运的信号机制报道的还不多,但是已经明确花后高温降低光合作用进而限制光合生产的物质供应,此时茎鞘物质运转增强,对产量贡献达到6%~100%[61]。然而,热胁迫下茎鞘NSC向籽粒的转运存在品种差异,品种的耐热性不仅与高温下保持较稳定的光合速率有关,更与其茎鞘NSC储存能力关系密切[62]。Wang等[63]研究指出花后高温减少了籽粒淀粉和果聚糖的含量,增加了B型淀粉粒的体积、数量和表面积的比例,降低了SST和FFT的活性;花前花后均高温与只花后高温相比产量明显提高;花前花后均高温较只花后高温具有较高的淀粉含量,进而具有较少的修饰B型淀粉粒大小指数。这表明,花前适当高温可以促进花后高温条件时茎鞘NSC向籽粒转运,减少了花后高温对籽粒淀粉含量和颗粒分布的影响,从而稳定了产量。

茎鞘NSC与热胁迫适应能力密切相关,这在水稻的研究中也得到验证[64]。Morita等[65]通过对水稻品种3年的研究发现,新品种Nikomaru较现有主导品种Hino-hikari产量提高7%~8%,其主要原因不是生物量和源库大小的差异,而是Nikomaru具有较高的转运率,这与其茎鞘NSC含量成显著正相关。表明,高温条件下NSC作为物质转运的主要来源对于维持较高产量具有重要意义。

小麦茎鞘NSC除与抗寒性、抗旱性以及耐热性密切相关外,相关研究表明茎鞘NSC,特别是果聚糖,对土壤贫瘠、盐碱、涝渍、寡照等非生物逆境胁迫具有一定适应性,对于维持非生物逆境下小麦产量稳定性具有重要意义。

3 栽培措施对茎鞘NSC的调控

小麦茎鞘NSC向籽粒的转运受到库强度、环境和品种3个因素的影响[66]。在一些环境相对较差地区,生产上通过调控茎鞘NSC含量进而提高小麦对逆境的适应能力已经得到广泛应用[67]。栽培措施对小麦茎鞘NSC的调控主要有品种选择、水分管理、氮肥运筹等方面。

3.1 品种选择

Bazargani等[68]通过对2个不同蛋白质组类型的小麦品种的研究发现,小麦或许是通过响应基因的表达促进茎鞘NSC向籽粒中的运转,以此适应干旱环境。

Rebetzke等[69]研究表明,具有较低株高和较早开花期的品种往往具有较高的茎鞘NSC含量。这是因为半矮杆品种降低了结构性碳水化合物需求,而光合面积相对稳定[70],光合速率相对较高[71],这有利于提高茎鞘NSC含量。同时,这类品种往往分蘖少但成穗强,具有较低的生物量,但较多地向籽粒分配保证了较高的收获指数[69]。而具有较长营养生长期的品种分蘖较多[72],增加了对结构性碳水化合物的需求,进而降低了贮存NSC的能力[69]。

具有较少粒数[73](亦有相反报道),或地上部具有较低蛋白质含量的品种往往具有较高的NSC含量[74]。主要原因:一是较多的分蘖增加了氮素吸收,形成较高的叶面积,减少了NSC的积累[69],穗快速发育期内,氮素积累和向籽粒的分配有利于每穗粒数的形成[69,75],具有较多粒数、较大库强度的品种有利于后期茎鞘NSC向籽粒的运转[76],穗含氮量较低的品种限制了每穗粒数的形成,但能贮存更多NSC[74,77];二是花原基分化期伴随着茎鞘伸长和NSC积累,因此NSC积累成为籽粒形成的潜在竞争库,导致花前向籽粒的物质供应受限[1,78]。

3.2 水分管理

水分管理的核心是一定水分供应条件下优化作物产量水平,进而提高单位耗水产量即水分利用效率。Passioura[79]将此总结为3个途径:充分利用水分达到无效耗水最小化;水碳高效生产达到生物量最大化;物质高效转运达到收获指数最大化。现行调亏灌溉主要是通过利用土壤储水、关键期低频灌溉、根区交替灌溉等方式大幅减少灌溉水,适当水分亏缺维持相对理想产量的一种水分管理方式[80]。

播前土壤水分状况与小麦早期生长势密切相关,Siddique等[81]指出早期生长势强的春小麦品种前期土壤蒸发耗水相对较少。Musick等[82]发现播前土壤水分与小麦产量为显著正相关,且比总耗水更显著。拔节期是小麦对水分最为敏感的时期[83],此时灌水有利于提高单位面积粒数[84-85],增加库强度,利于后期茎鞘NSC运转[84]。推迟拔节水可以促进提前开花[86],促进茎鞘NSC向籽粒运转而获得较高的收获指数,进而提高籽粒产量。近年来,一些地区由于花后衰老推迟引起的NSC转运不畅导致籽粒灌浆不足的问题在小麦和水稻生产中日渐引起关注[87]。灌浆期是产量形成的关键期,40%~50%的生物量在此阶段转运到籽粒当中。灌浆期适当干旱可以促进植株衰老,进而启动茎鞘NSC向籽粒运转[88]。

有关适当水分亏缺促进茎鞘NSC转运的调控机理前人

进行了大量研究。Goggin等[23]研究表明：干旱条件下茎鞘果聚糖含量提高，但FFT酶活性没有明显变化。花前，果聚糖含量与果聚糖转化酶存在正相关关系；花后，31%的果聚糖依然存在顶部第二节，尽管底部第二节间的FFT酶活性比其高5倍。Yang等[89]研究发现，小麦茎鞘FEH和SPS酶在花后适当水分亏缺下活性增强，促进NSC转运。在协调果聚糖和蔗糖的代谢酶活性中ABA起到了关键作用。Joudi等[90]对不同果聚糖积累转运特点的品种进行研究发现，干旱条件下，转运效率较高的品种产量较高，积累了更多的果聚糖，花后6-FEH活性增加较1-FEH明显，倒二节具有较高的6-FEH活性。由此说明，较高的转运效率和6-FEH活性有利于小麦对干旱环境的适应。

3.3 氮肥运筹

氮肥运筹在小麦生产中起着重要作用，氮肥用量和时期影响着物质积累和产量形成。过去20年，华北地区小麦产量有了很大提高，其中化肥，特别是氮肥的大量投入起到了非常重要的作用[91]。但是随着氮肥的大量施用，也带来产量稀释效应和生态环境的恶化。提高小麦氮肥利用效率是降低氮肥投入量同时维持产量的关键。

基于土壤-作物综合管理系统，即根层测土和植株吸氮，Chen等[92]提出国内小麦田间最优施氮量为220 kgN·hm^{-2}；Lu等[93]指出华北地区施用时期为播前和拔节期，其施肥分配比例约为1∶3.3。Bahrani等[94]对地中海气候条件下冬小麦研究指出，适当施用氮肥（80 kg·hm^{-2}）能提高小麦茎鞘NSC运转效率，特别是干旱条件下其转运效率达到最大，然而，进一步施氮肥（160 kg·hm^{-2}）延缓了花后衰老，降低了茎鞘NSC运转。花后干旱条件下，施氮肥80 kg·hm^{-2}时转运效率最高，进一步增施氮肥转运效率降低[94]。

氮素吸收过程中，随着更多的碳通过糖酵解转化成磷酸烯醇式丙酮酸，碳水化合物合成减少，进而进入有机酸代谢途径[95]。氮素影响碳氮代谢中的酶活性，包括有机酸合成酶的基因表达[96]；抑制腺苷二磷酸葡萄糖焦磷酸化酶活性，进而减少淀粉和蔗糖的合成[23]。作为一种抑制信号，氮素能迅速降低FTs酶活性进而减少果聚糖合成[97]。在氮素缺失时，6-SFT酶在果聚糖代谢中起重要作用[98]。由此可见，氮吸收与碳代谢相互协调，能转移更多的碳合成N代谢的中间产物，进而减少碳水化合物的合成[23]。Valluru等[99]研究发现，小麦茎鞘NSC含量与其根冠比、茎含氮量、叶含氮量、单位叶面积含氮量和营养器官干物质呈负相关关系。由此表明，植株氮含量是调控小麦茎鞘NSC含量的重要因素。低氮条件下，具有较高的营养器官干物质和旗叶宽度，以及较低的根冠比的品种往往具有较高的茎鞘NSC含量；然而在高氮条件下，具有较低的营养器官干物质和旗叶宽度的品种往往具有较高的茎鞘NSC含量。小麦茎鞘NSC含量与纤维素和半纤维素呈负相关关系，这表明减少茎鞘中结构性碳水化合物或许可以提高其茎鞘NSC含量。McIntyre等[100]研究发现淀粉与磷酸吡哆醛途径的氮素代谢相关，进一步分析^{12}C和N代谢相关的基因在不同水氮处理下的表达发现，其中2种N-氨基酸代谢基因的表达与NSC含量呈负相关关系。由此表明，吸收氮向氨基酸转变显著影响茎鞘NSC的含量。

此外，播期优化、合理密植和化控调节等栽培措施对茎鞘NSC转运也有很好的调节作用。

4 茎鞘NSC在遗传育种中的应用

茎鞘NSC在基因型间具有很大差异，据先前报道，开花初期其含量占茎鞘干重含量的比例为0.11~0.43[11,67]。Ruuska等[11]研究指出，小麦茎鞘NSC积累量具有较高的可遗传性（$H=0.90\pm0.12$），这表明定向选育较高或较低茎鞘NSC是可行的。澳大利亚和英国的育种家已经着手将这一目标性状转到现有种质资源中以期提高小麦对干旱胁迫的适应性[101,102]。

通过QTL定位分析发现，小麦茎鞘NSC的2个基因位点位于染色体1b和2A[15]。茎鞘NSC相关的基因位点有8~16个，总的NSC基因位点有4~8个[69]。编码茎鞘果聚糖合成酶的基因表达水平与茎鞘NSC含量和果聚糖含量密切相关[104]。随着茎鞘果聚糖向籽粒转运，1-FEH酶活性增强[104]。与FEH酶相关的QTL位点与控制粒重、NSC和灌浆速率位点存在共定位现象[89]。Zhang等[105]克隆了3个1-FET相关基因并鉴定一个同源染色体，该同源染色体被认为是调控FEH酶活性的主要基因，能促进果聚糖降解转运到籽粒当中。

小麦茎鞘NSC积累和转运与品种的形态特征密切相关，茎长度、茎直径、茎厚度均具有较高的可遗传性（$H=0.42\sim0.84$）[67]。因此，通过形态指标优化和筛选可以提高小麦品种茎鞘NSC含量进而提高其抗旱性。小麦品种间茎鞘伸张速率存在明显差异，因此优化穗发育阶段进而提高NSC积累显得尤为重要[106]。调控果聚糖合成与分解转录因子的相关基因也能实现调控NSC的分配。近来，小麦转录因子TaMYB13被发现是Ta1-SST和Ta6 SFT的转录启动因子，表明TaMYB13及其直系同源基因参与了果聚糖合成途径调控[107]。

综上，生产中应重视栽培措施，特别是品种选择、水分管理、氮肥运筹对茎鞘NSC的调控，发挥茎鞘NSC在抗逆稳产中的作用。此外，基于小麦茎鞘NSC积累转运的遗传学分析，综合运用传统育种和分子育种的方法发挥茎鞘NSC在小麦抗逆稳产中的作用具有重要意义。

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Review on metabolism and regulation of non- structural carbohydrates in wheat stem

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Abstract With the decrease of the photosynthetic rate under stress, non-structural carbohydrates (NSC) in wheat stem become the main carbon source, accounting for 20%~50%, for grain filling. Therefore, it is very important understanding the NSC metabolic regulation and the effect of the cultivation management and the genetic improvement on the NSC metabolism for adequately using the NSC for high or stable yield in wheat under stress conditions. In this review, the fructosan, as the predominant component of the NSC in the wheat stem, is taken as an example to reveal its metabolic pathway, including the structure and the synthesis, as well as the transportation and the degradation. The role of the NSC in the wheat stem is analyzed under stress conditions, especially at low and high temperature, and in drought. The regulation effect of the cultivation managements on the NSC is discussed, such as those related with the cultivar election, the water and the nitrogen management. Finally, the application prospect of the wheat stem NSC in breeding for stress tolerance is discussed.

Keywords abiotic stress; stress tolerance; yield; cultivation management; genetic improvement

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