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不同氮效率油菜 SPS 和 PEPC 活性差异及其对籽粒产量与油分含量的影响

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摘要:【目的】蔗糖磷酸合成酶(sucrose phosphate synthase,SPS)与磷酸烯醇式丙酮酸羧化酶(phosphoenolpyruvate carboxylase,PEPC)分别控制着植物体内的碳骨架向碳代谢和氮代谢的流转,影响作物的产量与品质。为探明氮高效油菜品种在高效利用氮素的同时协调籽粒蛋白与油分累积矛盾的机理,研究了不同氮效率油菜品种的 SPS 与 PEPC 活性差异及其对籽粒油分含量的影响。**【方法】**采用土培试验,以氮高效品种 27 号(H)与氮低效品种 6 号(L)为试验材料,在常氮(N)与低氮(S)条件下,研究不同氮效率油菜品种苗期到花期叶片与角果发育初期的角果、角果发育中期的角果皮与籽粒中 SPS 与 PEPC 活性变化及差异、生长后期碳素转运量与转运率以及收获期籽粒油分含量的差异。**【结果】**两种供氮水平下,氮高效品种 27 号的产量与籽粒油分含量均显著高于氮低效品种 6 号,品种优势明显;且氮高效品种 27 号苗期到花期叶片与角果发育初期的角果、角果发育中期的角果皮与籽粒中的 SPS 与 PEPC 活性均高于氮低效品种 6 号,两种供氮水平的规律相同,但是 SPS 与 PEPC 活性的比值(SPS/PEPC)却因生育期不同而异,营养生长期叶片中氮高效品种 27 号的 SPS/PEPC 高于氮低效品种 6 号,开花期品种间叶片 SPS/PEPC 相近,角果发育期主要生殖器官中的 SPS/PEPC 值氮高效品种反而低于氮低效品种。说明氮高效品种向碳代谢和氮代谢输送的碳骨架在全生育期均多于氮低效品种,而碳代谢对氮代谢的响应只在生育前期强于氮低效品种,生育后期则相反。碳素转运量与转运率、籽粒油分含量与产量也是氮高效品种大于氮低效品种,这可能为氮高效品种协调籽粒蛋白与油分累积矛盾的重要生理机制。供氮水平对上述各指标有不同的影响,籽粒产量、PEPC 活性、碳素转运量及转运率以常氮处理高于低氮处理,而油分含量、SPS 活性及 SPS/PEPC 以常氮处理低于低氮处理,但不改变以上指标的品种间差异。**【结论】**与氮低效品种相比,氮高效品种全生育期向碳、氮代谢均输送更多的碳骨架,这是氮高效品种缓解碳、氮代谢矛盾的重要前提;碳代谢对氮代谢的响应生育前期较高、生育后期较低,同时生育后期有更多营养器官的碳素转运到籽粒,也为油菜生育后期满足籽粒碳、氮代谢所需要的碳骨架,并协调籽粒油分与蛋白质含量的矛盾提供了条件。

关键词: 油菜; SPS; PEPC; 碳氮代谢; 籽粒油分
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Different activities of SPS and PEPC in oilseed rape with different nitrogen use efficiency and their influence on seed yield and oil-content

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Abstract:【Objectives】 Transportation of carbon skeleton into carbon metabolism pathway and nitrogen metabolism circulation were respectively controlled by SPS (sucrose phosphate synthase) and PEPC

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(phosphoenolpyruvate carboxylase), and then the yield and grain quality of crop were affected by the two enzymes. In order to elucidate the regulation mechanism of contradiction between seed protein and oil during the high nitrogen use efficiency (NUE) progress in oilseed rape with high N efficiency, the different activities of SPS and PEPC and their influence on seed yield and oil content in oilseed rape with different NUE were studied in this paper. **【Methods】** Variety No. 27 with high NUE (H) and variety No. 6 with low NUE (L) were cultured in soil under different nitrogen conditions [normal nitrogen condition (N) and nitrogen stress condition (S)] to study the difference of enzyme activities (SPS and PEPC) in leaf from seedling stage to flowering stage, in silique at early silique stage and in grain and silique husk at silique mid-term stage between the two NUE rape varieties as well as carbon (C) transportation amount and rate and their seed yield and seed oil content. **【Results】** The test results showed that seed yield and seed oil content of high NUE (No. 27) variety were significantly higher than those of low NUE (No. 6) variety under two nitrogen conditions (normal nitrogen and nitrogen stress), the high NUE rape showed obvious variety advantage. Moreover, activities of SPS and PEPC of high NUE (No. 27) variety in leaf from seedling stage to flowering stage were higher than those of low NUE (No. 6) variety under two nitrogen conditions, the same tendency was found in silique at early silique stage as well as in grain and silique husk at silique mid-term stage. While the SPS/PEPC of the two variety rape was changed at different growth periods, SPS/PEPC of high NUE (No. 27) variety in leaf at vegetative stage was higher than those of low NUE (No. 6) variety, SPS/PEPC of the two varieties rape was similar in leaf at flowering stage, instead SPS/PEPC in main reproduction organs at silique stage of high NUE (No. 27) variety was lower compared to low NUE (No. 6) variety, which revealed that amount of delivery of carbon skeleton to C metabolism and N assimilation of high NUE (No. 27) variety was more than those of low NUE (No. 6) variety during the whole growth period and the response of C metabolism to N assimilation of high NUE (No. 27) variety was higher than those of low NUE (No. 6) variety at early growth stage, while at late growth stage the response of response of high NUE (No. 27) variety was lower than that of low NUE (No. 6) variety. Meanwhile C transportation amount and rate of high NUE (No. 27) variety were significantly higher than those of low NUE (No. 6) variety, which might be the vital physiological mechanism that regulating the contradiction between seed protein and oil during the high nitrogen use efficiency (NUE) progress in oilseed rape with high N efficiency. As for influence of different nitrogen conditions on items which we tested above, the results showed that seed yield, activity of PEPC, carbon transportation amount and rate were higher under normal nitrogen condition than under nitrogen stress condition, but seed oil content, activity of SPS, SPS/PEPC showed an inverse law, these phenomena appeared in the two rape varieties. **【Conclusions】** Compared to low NUE (No. 6) variety, more carbon skeleton was transported into C and N metabolism pathway in high NUE (No. 27) variety during the whole growth stage. This was the important premise for HNUE variety to coordinate the contradiction between C and N metabolisms. Response of C metabolism to N assimilation was higher during earlier growth stage than during later growth stage. Meanwhile, higher proportion of C in vegetative organs was transported into seed during later growth stage, which met the demands of carbon skeleton in C and N metabolism and coordinated the contradiction between seed oil and protein contents during later growth stage.

Key words: *Brassica napus* L.; SPS; PEPC; carbon nitrogen metabolism; seed oil

碳与氮是作物体内两大重要元素,参与作物生命活动中化合物的形成,对作物产量与品质的形成起重要作用。碳、氮代谢对于作物的生长发育尤为重要,其最首要的功能是为细胞的新陈代谢提供碳骨架与能量[1-2],其中氮代谢可为合成蛋白质与核酸等重要生命物质提供氮源[3]。碳、氮代谢二者密不可分,其相互作用是作物产量与品质的基石[4],同时碳、氮代谢作为植物体内的两大主要代谢过程,对代谢途径所需要的碳骨架与能量存在着明显的竞争[5]。因此,作物生长过程中调节碳和能量的流向,以最大限度地同时满足碳、氮代谢的需求,达到作物优质高产是十分重要的[6]。研究表明,蔗糖磷酸合成酶(sucrose phosphate synthase, SPS)与磷酸烯醇式丙酮酸羧化酶(phosphoenolpyruvate carboxylase, PEPC)在碳和能量的流转过程中起重要作用,二者共同调节着光合作用固定的碳在糖类与氨基酸之间的分配[7-8],从而调节碳、氮代谢的方向。SPS 为植物体蔗糖合成的关键调控酶,在控制

蔗糖合成速率的同时,平衡光合作用物质合成、蔗糖运输与淀粉形成等过程;PEPC 具有固定 CO_2 为 C_3 循环提供碳源的重要作用,同时 PEPC 还可促进并调节有机酸合成,为氮代谢途径提供碳骨架和能量[9-10],在油菜等 C_3 植物中则以后一个作用为主。油菜是油料作物,碳、氮代谢竞争导致的籽粒蛋白质与油分含量之间的矛盾比较突出,较好的氮素营养条件,虽可提高产量和籽粒蛋白质含量,但减少籽粒油分含量。因此,如何调节油菜碳、氮代谢的关系,在保证籽粒形成过程所需的基本氮代谢需求的前提下,使碳骨架及时流向碳代谢方向是人们关注的问题。陈历儒等[11]研究表明,氮高效油菜品种并没有因高效吸收利用氮素而降低油分含量,说明其中存在着较好的碳、氮代谢协调机理,但这一协调机理是否和 SPS 与 PEPC 的活性有关,目前尚未见相关报道。本试验对不同氮效率油菜品种的 SPS 与 PEPC 酶活性及其与籽粒油分的关系进行研究,以期为揭示油菜碳、氮代谢方向调节对籽粒油分形成的影响机理提供参考。

1 材料与方法

1.1 材料及试验设计

试验于 2013 年 9 月至 2014 年 3 月在湖南农业大学耘圆基地进行,供试土壤为第四纪红土母质发育的冲积菜园土,其有机质含量 23.08 g/kg、全氮 1.53 g/kg、全磷 1.33 g/kg、全钾 19.79 g/kg、碱解氮 129.0 mg/kg、速效磷 79.7 mg/kg、速效钾 137.4 mg/kg、pH 5.18。供试油菜品种为本课题组经过大田试验筛选出的氮高效品种 27 号(No. 27)和氮低效品种 6 号(No. 6),其中氮高效品种的氮素吸收与利用效率以及籽粒中氮素积累量均高于氮低效品种。本试验采用盆栽土培试验,用 30 cm×20 cm 白瓷钵,每钵装土 6.25 kg,栽植 1 株,采用育苗移栽方法,于 2013 年 8 月 25 日大田育苗,9 月 25 日移栽,完全随机区组排列。试验设品种与氮水平两个因子,氮水平设正常供氮与低氮两个水平,共 4 个处理,分别为:高效品种正常供氮(H-N);高效品种低氮(H-S);低效品种正常供氮(L-N);低效品种低氮(L-S)。每处理重复 24 次(每处理每次取样重复 4 次),共 96 钵。正常供氮处理每公斤土施 N 0.2 g、P_2O_5 0.1 g、K_2O 0.15 g、B 0.0024 g;低氮处理除不施氮肥外,其余养分施用量与正常供氮处理相同。氮肥用尿素(含 N 46%)、磷肥用钙镁磷肥(含 P_2O_5 12%)、钾肥用氯化钾(含 K_2O 60%)、硼肥用硼砂(含 B 10.8%)。

1.2 取样及测定方法

分别在油菜苗期、抽薹期、开花期、角果发育初期、角果发育中期与收获期取整株样品,其中前 5 个时期样品洗净、吸干水分后称鲜重;苗期、抽薹期与开花期取长势健壮的叶片、角果发育初期及角果发育中期选取同一生长梯度的角果用于测定蔗糖磷酸合成酶(sucrose phosphate synthase, SPS)和磷酸烯醇式丙酮酸羧化酶(phosphoenolpyruvate carboxylase, PEPC)活性,剩余部分烘干,烘干后的所有样品粉碎过筛测定植株全碳含量;收获期样品烘干后测定全碳和籽粒产量与籽粒油分含量。

SPS 活性用可见分光光度法测定[12];PEPC 活性用紫外分光光度法测定[13];籽粒油分含量用索氏提取法测定[14];植株总碳用 Vario PYRO cube 元素分析仪(Elemental 公司)测定。根据植株总碳测定结果,以营养器官中总碳累积量最高的生育期为基准(本试验中为抽薹期)用差减法计算碳素转运量与转运率[15]。计算公式为:

碳素转运量(mg) = 抽薹期植株碳素累积量 - 收获期营养器官碳素累积量

碳素转运率(%) = 碳素转运量/抽薹期植株碳素累积量 ×100

1.3 数据处理

试验数据均用 Excel 和 SPSS 15.0 专业版统计软件进行处理。

2 结果与分析

2.1 不同氮效率油菜籽粒的产量与油分含量

2.1.1 籽粒产量　由图 1 可以看出,品种与供氮水平对籽粒产量有显著影响,无论氮水平高低,氮高效品种 27 号的籽粒产量均显著高于氮低效品种 6 号。与正常供氮相比,两品种均表现为低氮水平下籽粒产量显著降低。

2.1.2 籽粒油分含量　图 2 显示,无论氮水平高低,品种 27 号的籽粒油分均高于品种 6 号,差异显著;不同供氮水平,两品种均表现为低氮处理时籽粒油分含量显著高于正常供氮。即氮高效品种具有更高的油分积累能力,低氮条件下有利于籽粒油分含量的累积,这是因为缺氮时氮代谢减弱,相应地有更多的碳骨架流向碳代谢。但因为缺氮时籽粒产量下降,总油分产量不会提高。

2.2 不同氮效率油菜 SPS 与 PEPC 活性的差异

2.2.1 油菜 SPS 活性　SPS 是作物碳水化合物积累

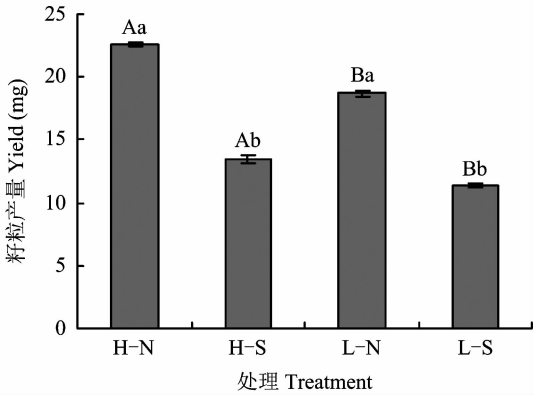

图 1　不同氮水平对两油菜品种籽粒产量的影响

Fig. 1　Seed yield of the two rape varieties in different nitrogen conditions

[注(Note)：柱上不同大写字母表示同一氮水平不同品种处理间差异达 5% 显著水平 Different capital letters above the bars indicate that differences between varieties are significant under same nitrogen condition at 5% level；不同小写字母表示同一品种不同氮水平处理间差异达 5% 显著水平 Different lowercase letters above the bars indicate that differences of same variety between nitrogen conditions are significant at 5% level.]

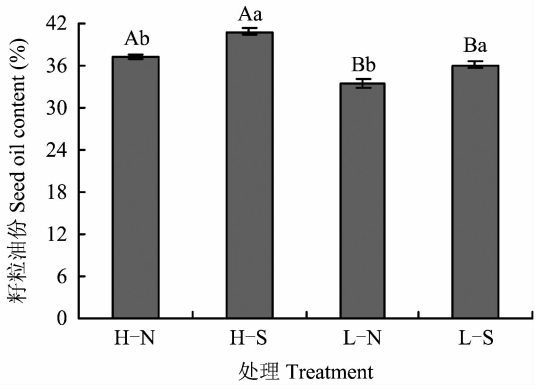

图 2　不同氮水平对两油菜品种籽粒油分含量的影响

Fig. 2　Seed oil content of the two rape varieties in different nitrogen conditions

[注(Note)：柱上不同大写字母表示同一氮水平不同品种处理间差异达 5% 显著水平 Different capital letters above the bars indicate that differences between varieties are significant under same nitrogen condition at 5% level；不同小写字母表示同一品种不同氮水平处理间差异达 5% 显著水平 Different lowercase letters above the bars indicate that differences of same variety between nitrogen conditions are significant at 5% level.]

的关键酶。由表 1 可知，两种供氮水平下，叶片 SPS 活性品种 27 号高于品种 6 号，苗期、抽薹期、开花期呈现相同规律，两品种苗期与抽薹期的酶活性差异达到了显著水平，开花期差异不显著；角果发育初期的角果、角果发育中期的角果皮和籽粒中的 SPS 活性也表现为品种 27 号高于品种 6 号，角果与籽粒中的酶活性差异达到了显著水平。

观察不同供氮水平对 SPS 活性的影响，表明两品种均表现为低氮处理高于正常供氮处理，所有生育期规律一致，其中品种 27 号苗期叶片与角果发育初期角果中的酶活性差异也达到了显著水平。与苗期和抽薹期相比，所有处理的开花期叶片的 SPS 活性明显下降，说明进入生殖生长期以后油菜营养器官的基本干物质积累大幅度减弱。

表 1　不同氮素供应条件下不同油菜品种的 SPS 活性[mg/(g·h), FW]

Table 1　SPS activity of two rape varieties in different nitrogen conditions

品种与处理 Variety and treatment		叶片 Leaf			角果发育初期 Early silique stage	角果发育中期 Silique mid-term stage	
		苗期 Seedling stage	抽薹期 Bolting stage	开花期 Flowering stage	角果(角果皮+籽粒) Silique (grain + husk)	籽粒 Grain	角果皮 Silique husk
27 号	H-N	187.4 Ab	207.2 Aa	10.73 Aa	168.6 Aa	395.8 Aa	141.2 Aa
No. 27	H-S	331.2 Aa	247.7 Aa	12.48 Aa	226.9 Aa	418.3 Aa	166.0 Aa
6 号	L-N	93.99 Bb	145.4 Ba	7.601 Aa	131.1 Ba	319.3 Ba	100.0 Aa
No. 6	L-S	188.8 Ba	163.4 Ba	10.40 Aa	153.7 Ba	360.7 Ba	149.2 Aa

注(Note)：数据后不同大写字母表示同一氮水平不同品种处理间差异达 5% 显著水平 Values followed by different capital letters indicate that differences between varieties are significant under same nitrogen condition at 5% level；数据后不同小写字母表示同一品种不同氮水平处理间差异达 5% 显著水平 Values followed by different lowercase letters indicate that differences of same variety between nitrogen conditions are significant at 5% level.

2.2.2 油菜 PEPC 活性　PEPC 可为作物氮代谢提供碳骨架。由表 2 可以看出，两种供氮水平下，叶片 PEPC 活性以品种 27 号高于品种 6 号，苗期、抽薹期、开花期呈现相同规律，其中正常供氮处理下苗期与开花期 PEPC 活性品种间的差异达到了显著水平；无论供氮水平高低，角果发育初期的角果、角果

表2 不同氮素供应条件下不同油菜品种PEPC活性[μg/(mg·min)]

Table 2 PEPC activity of two rape varieties in different nitrogen conditions

品种与处理 Variety and treatment		叶片 Leaf			角果发育初期 Early silique stage	角果发育中期 Silique mid-term stage	
		苗期 Seedling stage	抽薹期 Bolting stage	开花期 Flowering stage	角果(角果皮+籽粒) Silique (grain+husk)	籽粒 Grain	角果皮 Silique husk
27号 No. 27	H-N	1.1296 Aa	1.1414 Aa	1.5786 Aa	1.7657 Aa	1.5597 Aa	1.1824 Aa
	H-S	0.6872 Ab	0.9682 Ab	0.7431 Ab	1.5404 Aa	1.0744 Ab	0.9738 Ab
6号 No. 6	L-N	0.8388 Ba	1.0145 Aa	1.1198 Ba	1.5929 Ba	1.2553 Ba	1.1489 Aa
	L-S	0.6221 Aa	0.9192 Aa	0.4377 Ab	0.8892 Ab	0.8332 Bb	0.9089 Ab

注(Note):数据后不同大写字母表示同一氮水平不同品种处理间差异达5%显著水平 Values followed by different capital letters indicate that differences between varieties are significant under same nitrogen condition at 5% level;数据后不同小写字母表示同一品种不同氮水平处理间差异达5%显著水平 Values followed by different lowercase letters indicate that differences of same variety between nitrogen conditions are significant at 5% level.

发育中期的角果皮与籽粒中的PEPC活性均以品种27号高于品种6号,其中正常供氮处理下的角果和两种供氮水平下籽粒中的PEPC酶活性两品种之间差的异也达到了显著水平。

不同供氮水平对PEPC活性的影响显示,所有生育期两品种均表现为正常供氮高于低氮处理,除品种27号在角果发育期的角果和品种6号苗期与抽薹期叶片的PEPC活性差异不显著之外,其余均达到了差异显著水平。

2.3 不同氮效率油菜SPS/PEPC比值的差异

SPS/PEPC比值表明单位PEPC活性变化所对应的SPS活性变化,可表征碳代谢对氮代谢变化的响应情况,由表3可以看出,营养生长期叶片SPS/PEPC在两种供氮水平下均表现为品种27号高于品种6号,差异显著;而开花期叶片SPS/PEPC两品种差异较小;角果发育期的SPS/PEPC,除正常供氮角果发育中期角果皮中SPS/PEPC以品种27号高于品种6号之外,其余处理下SPS/PEPC均为品种27号低于品种6号,低氮处理下角果与角果皮、两种供氮处理下籽粒中的SPS/PEPC值品种间差异达到显著水平。说明氮代谢加强时碳代谢相应加强的程度在营养生长期以氮高效品种明显高于氮低效品种,到开花期则两品种趋于接近,角果发育期氮高效品种反而低于氮低效品种。这是因为氮高效品种的籽粒油分含量高于氮低效品种,显然氮高效品种在角果发育期SPS/PEPC值较低的情况下应该另有补充碳素的途径。供氮水平对SPS/PEPC也有影响,主要表现为低氮条件下的SPS/PEPC值升高。

表3 不同氮水平下两品种SPS/PEP比值

Table 3 SPS/PEPC of two varieties under different nitrogen conditions

品种与处理 Variety and treatment		叶片 Leaf			角果发育初期 Early silique stage	角果发育中期 Silique mid-term stage	
		苗期 Seedling stage	抽薹期 Bolting stage	开花期 Flowering stage	角果(角果皮+籽粒) Silique (grain+husk)	籽粒 Grain	角果皮 Silique husk
27号 No. 27	H-N	206.2 Ab	174.4 Ab	7.64 Ab	52.12 Aa	311.08 Ba	151.42 Aa
	H-S	510.9 Aa	315.1 Aa	16.77 Aa	71.4 Ba	384.97 Ba	117.45 Ba
6号 No. 6	L-N	114.2 Bb	143.7 Bb	6.81 Ab	61.22 Ab	551.19 Aa	75.38 Bb
	L-S	334.8 Ba	193.7 Ba	18.80 Aa	148.07 Aa	596.08 Aa	147.66 Aa

注(Note):数据后不同大写字母表示同一氮水平不同品种处理间差异达5%显著水平 Values followed by different capital letters indicate that differences between varieties are significant under same nitrogen condition at 5% level;数据后不同小写字母表示同一品种不同氮水平处理间差异达5%显著水平 Values followed by different lowercase letters indicate that differences of same variety between nitrogen conditions are significant at 5% level.

2.4　不同氮效率碳素转运量与转运率的变化

碳素转运量与转运率表示油菜生育前期营养器官所积累的碳素向生殖器官所转运的情况。本试验中营养器官累积的碳素以抽薹期最高，因此，本文用抽薹期和收获期营养器官总碳计算碳素转运量与转运率。图 3 表明，收获期两种供氮处理下碳素转运量与转运率均为品种 27 号大于品种 6 号，差异皆达到了显著水平，说明品种 27 号具有更高的碳素转运能力；比较不同供氮水平，两品种皆表现为正常供氮处理下碳素转运量与转运率大于低氮处理，差异也达到了显著水平。

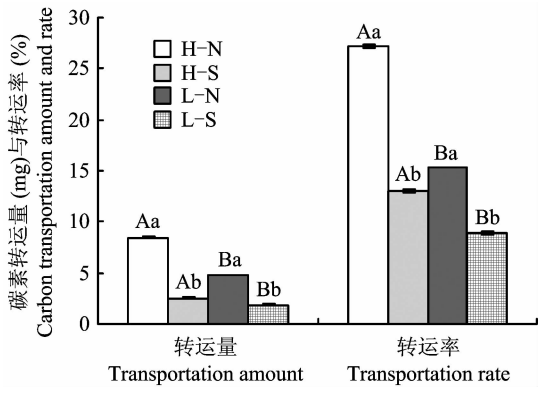

图 3　不同氮水平下两油菜品种碳转运量与转运率

Fig. 3　Carbon transportation amount and rate of two rape varieties under different nitrogen conditions

[注(Note)：柱上不同大写字母表示同一氮水平不同品种处理间差异达 5% 显著水平 Different capital letters above the bars indicate that differences between varieties are significant under same nitrogen condition at 5% level；不同小写字母表示同一品种不同氮水平处理间差异达 5% 显著水平 Different lowercase letters above the bars indicate that differences of same variety between nitrogen conditions are significant at 5% level.]

3　讨论

3.1　不同氮效率油菜品种 SPS 与 PEPC 活性差异及其对籽粒产量与油分含量的影响

碳、氮代谢决定油菜的产量与品质，碳代谢与氮代谢竞争光合作用产生的碳架与还原力，而 SPS 与 PEPC 在碳、氮代谢交汇点对碳架在碳、氮代谢间的分配及二者代谢方向的调节中起重要作用，SPS 促进碳骨架向碳代谢方向运输，而 PEPC 促进碳骨架运往氨基酸形成途径[16-17]。唐湘如等[18]研究表明，SPS 活性高有利于油菜籽粒油分的积累；Rademacher 等[19]将 PEPC 基因转入土豆后发现，碳素流动直接从糖类与淀粉的合成转入苹果酸与氨基酸的合成。以上研究已从不同角度证明了 SPS 与 PEPC 活性对碳、氮代谢带来的影响，但是不同氮效率作物品种之间 SPS 与 PEPC 活性差异及其对作物产品品质影响的研究目前报道还很少。本试验中氮高效品种的籽粒产量与油分含量高，且叶片及角果的 SPS 与 PEPC 活性均高于氮低效品种，即无论是营养生长期还是生殖生长期，氮高效品种均可以向碳代谢与氮代谢输送更多的碳骨架与能量，氮高效品种的碳(氮)代谢加强，并没有以抑制氮(碳)代谢为代价的，这是氮高效品种氮素吸收利用效率高、籽粒累积蛋白质多，但并没有降低籽粒产量与油分含量的物质基础，当然其前提是氮高效品种具有更高的光合能力[20]。本试验还表明，供氮水平也影响 SPS 与 PEPC 活性，低氮时，两个品种的 SPS 活性皆升高，PEPC 活性皆降低，与唐湘如等[18]和罗凤等[21]的研究结果一致。低氮条件下 SPS 与 PEPC 活性的以上变化使氮代谢相对减弱，碳代谢相对加强，但是过弱的氮代谢会抑制油菜的正常生长和产量形成，从而导致籽粒油分含量提高、产量却降低的现象。因此，调节碳氮代谢方向，使更多的碳骨架流向碳代谢，必需在保证基本氮代谢的基础上进行，才可达到既提高产量又提高油分含量的目的。

3.2　不同氮效率品种油菜 SPS/PEPC 差异及其对油菜籽粒产量与油分含量的影响

SPS/PEPC 可反映氮代谢加强时相应的碳代谢强化能力，即碳代谢对氮代谢的响应能力，该能力强，向碳代谢输送碳的能力强，反之亦然。已有研究表明，SPS/PEPC 降低，更多光合碳化物分配至氨基酸从而增强氮代谢[22]，但以上研究还没有涉及 SPS/PEPC 与籽粒品质的关系。本试验计算的 SPS/PEPC 结果表明，营养生长期氮高效品种高于氮低效品种，开花期两品种相近，角果发育期氮高效品种反而低于氮低效品种，即碳代谢对氮代谢的响应能力，油菜生长前期氮高效品种大于氮低效品种，生长后期则相反，而且上述变化过程基本与生殖生长进程相吻合。那么，油菜生长后期氮高效品种累积更多油分的碳素来自何方？邹娟等[23]指出，油菜苗期是物质积累的主要时期，其决定着籽粒产量的形成，Severine 等[24]指出，油菜生育后期籽粒形成所需的干物质有很大一部分来自生育前期积累的转运，生育前期叶片中蔗糖合成能力决定着后期的产量。本试验用差减法计算了生育后期营养器官碳素的转运量，结果表明，氮高效品种生育后期由营养器官向籽粒的碳素转运量和转运率均高于氮低效品种。可见，营养生长期氮高效品种不仅向碳、氮代谢输送的

碳骨架多,碳代谢对氮代谢变化的响应度也高,而到生殖生长期,营养生长与生殖生长并行,碳、氮代谢之间的矛盾加剧,氮高效品种仅保证向碳、氮代谢输送更多的碳骨架,碳代谢对氮代谢变化的响应度降低,由此不足的碳素由茎叶等营养器官的碳素转运来补充,这种方式有利于缓解生殖生长期角果和籽粒中碳、氮代谢对碳骨架的竞争,从而为协调籽粒油分与蛋白质含量的矛盾并提高产量提供了条件。

4 结论

1)氮高效油菜品种的籽粒产量与油分含量均高于氮低效品种。

2)氮高效油菜品种的SPS与PEPC活性全生育期皆高于氮低效品种,说明氮高效品种向碳代谢和氮代谢输送的碳骨架全生育期均多于氮低效品种,这是氮高效品种协调籽粒油分与蛋白质含量矛盾的重要物质基础。

3)氮高效油菜品种的SPS/PEPC值生育前期较高,生育后期较低,同时生育后期营养器官有更多的碳素转运到籽粒,这为油菜生育后期同时满足籽粒碳、氮代谢所需的碳骨架,进而为协调籽粒油分与蛋白质含量的矛盾提供了条件。

4)供氮水平并不改变以上指标在品种间的差异,但对上述各指标分别产生不同的影响,籽粒产量、PEPC活性、碳素转运量及转运率以正常供氮高于低氮处理,而油分含量、SPS活性及SPS/PEPC值则为正常供氮低于低氮处理。

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