

番茄嫁接苗根穗互作对其耐冷性的影响

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摘要: 以耐冷性强的番茄‘060112’(R)和冷敏感番茄‘060911’(S)为试材, 采用靠接法进行嫁接, 形成双根双穗嫁接苗RS/RS, 嫁接苗成活后, 通过断根或断穗, 设RS/RS、RS/R、RS/S、R/RS、R/S、R/R、S/RS、S/R、S/S共9个处理, 置于光强22 klx、光周期12 h/12 h的光照培养箱内, 测定昼夜温度10 °C/3 °C低温胁迫9 d及25 °C/15 °C常温恢复3 d过程中嫁接苗的冷害指数、根系活力、电解质渗透率及渗透调节物质含量, 探讨番茄根系、接穗及其互作效应对嫁接苗耐冷性的影响。经统计分析表明, 低温胁迫过程中, 具“R”根系或接穗的嫁接苗组合中, 以R/R处理冷害指数较低, 而具“S”根系或接穗的嫁接苗组合中, 以S/S处理的冷害指数较高, 同时R/R的叶片及根系电解质渗透率最低, 可溶性糖及脯氨酸含量最高, R/RS、RS/R、RS/S、S/RS等处理的冷害指数、电解质渗透率、可溶性糖及脯氨酸含量均介于R/R与S/S之间, 表明冷敏感的S根系或接穗均降低了嫁接苗中R的耐冷性, 而耐冷性强的R根系或接穗均提高了嫁接苗中S的耐冷性。RS/RS处理的耐冷性高于S/RS而低于R/RS, 表明根系在增强嫁接苗耐冷性中的作用大于接穗; 而具“RS”根或穗的嫁接苗中, 以RS-R的耐冷性显著高于RS-S, 且互作效应的P值小于0.01, 表明根、穗对嫁接苗耐冷性存在显著的互作效应。低温胁迫处理前, 不同耐冷性番茄根系活力、根系及叶片电解质渗透率、可溶性糖及脯氨酸含量等无显著差异, 但低温胁迫9 d后, 常温恢复3 d时, 不同处理间均表现出显著差异。

关键词: 番茄; 砧木; 嫁接; 低温胁迫; 耐冷性

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Effects of Rootstock and Scion Interaction on Chilling Tolerance of Grafted Tomato Seedlings

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Abstract: In order to investigate the effect of tomato rootstock, scion and their potential interaction on chilling tolerance, we grafted chilling-sensitive tomato cultivar ‘060911’ (S) and chilling-resistant tomato

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cultivar '060112' (R). We then selectively removed rootstock or scion from the grafted seedlings RS/RS, and incubated the newly formed 9 kinds of seedlings, *i.e.*, RS/RS, RS/R, RS/S, R/RS, S/RS, S/R, R/S, R/R, S/S in the growth chamber with light intensity of 22 klx and photoperiod 12 h/12 h. The seedlings were treated with low temperature at 10 °C/3 °C for 9 days and recovered at 25 °C/15 °C for 3 days. Chilling injury index, root activity, electrolyte leakage and osmotic adjustment substances were measured after the chilling treatment and after the recovery. Grafted seedlings behaved similarly in root activity, electrolyte leakage of root and leaf, soluble sugar and proline content before the chilling treatment, but showed significant difference after the chilling treatment and after the recovery. Among these 9 kinds of grafted seedlings, S/S seedlings displayed the highest while R/R seedlings displayed the lowest chilling injury index. Meanwhile, R/R seedlings showed the lowest electrolyte leakage, and the highest content of soluble sugar and proline. Meanwhile, R/R seedlings showed the lowest electrolyte leakage, and the highest content of soluble sugar and proline. While R/RS, RS/R, RS/S, S/RS seedlings were intermediate between R/R and S/S regarding the chilling injury index, electrolyte leakage, soluble sugar and proline content. Results indicated that both rootstock and scion are important for chilling tolerance. We further found that rootstock conferred higher chilling resistance than scion, due to the fact that the chilling tolerance of RS/RS was higher than that of S/RS, but lower than R/RS. Moreover, the chilling tolerance of RS-R was significantly higher than that of RS-S, and the *P* value of interaction was less than 0.01. The results showed that rootstock and scion had significant interaction effect on the chilling tolerance of grafted seedlings.

Keywords: tomato; rootstock; grafting; low temperature stress; cold resistance

番茄 (*Solanum lycopersicum* L.) 是中国冬春设施栽培面积最大的喜温性蔬菜之一, 易受低温弱光的影响, 导致其生长发育缓慢, 产量品质下降 (王丽娟 等, 2006)。而嫁接栽培在增强作物抗逆性 (于贤昌 等, 1997; Venem et al., 2008; Schwarz et al., 2010), 促进植株生长发育 (Francisco et al., 2010) 等方面具有重要作用。Gao 等 (2008, 2016) 的研究表明, 低温胁迫下, 茄子嫁接苗叶片的冷害指数及电解质渗透率显著低于自根苗, 脯氨酸及可溶性蛋白含量显著高于自根苗, 耐冷性明显增强。Liu 等 (2014) 在烟草上的研究表明, 抗性砧木嫁接苗叶片脯氨酸含量升高, 抗旱能力显著增强。Xing 等 (2014) 采用耐盐性强的南瓜砧木嫁接黄瓜, 可显著提高叶片可溶性糖含量, 有效缓解盐胁迫对嫁接苗生长的抑制作用。Li 等 (2008) 研究则发现, 耐冷性强的黄瓜砧木嫁接苗根系活力增加, 耐冷性增强。因嫁接苗是由来自不同个体的根系及接穗组成的复合体, 接穗生长所需的水分和矿质元素需要根系提供, 根系生长所需的碳水化合物则依靠接穗供给, 因此, 接穗不可避免地也会影响嫁接苗的生理特性和生长发育。Etehadnia 等 (2008) 研究发现, 耐盐性强的马铃薯接穗嫁接苗的耐盐性显著增强, Martinez-Rodriguez 等 (2008) 在番茄上及 Ai 等 (2010) 在黄瓜上的研究结果一致。前人的研究还表明, 砧木和接穗均可显著影响黄瓜 (于贤昌 等, 1998)、茄子 (张晓艳和徐坤, 2009) 嫁接苗的抗冷性, 以及大豆 (Serraj & Sinclair, 1996)、葡萄 (Tramontini et al., 2013) 嫁接苗的抗旱性。可见, 砧木和接穗均可对嫁接苗的抗逆性产生显著影响。但关于根、穗及其互作效应在增强番茄嫁接苗耐冷性方面各自作用的大小并不清楚。为此, 本试验中以耐冷性显著不同的 2 个番茄砧木为试材, 研究互为根、穗不同组合嫁接苗在低温胁迫条件下植株冷害指数、根系活力、电解质渗透率、渗透调节物质含量的变化, 明确根系、接穗及其互作效应在增强番茄嫁接

苗耐冷性中的作用大小, 为低温季节番茄嫁接栽培合理选用根穗品种提供理论依据。

1 材料与amp;方法

1.1 试验材料与amp;设计

试验于 2015—2016 年在山东农业大学进行。供试材料为耐冷番茄 ‘060112’ (R) 和冷敏感番茄 ‘060911’ (S)。种子催芽后播种于 108 孔穴盘内, 浇 Hoagland’s 营养液培养至五叶一心时, 采取靠接法嫁接, 组成双根双穗嫁接苗, 移栽于 32 孔穴盘内继续培养。

嫁接苗恢复生长后, 通过断根或断穗, 形成 9 个不同的 “根/穗” 组合处理 (R/R、R/RS、R/S、RS/R、RS/RS、RS/S、S/R、S/RS、S/S)。每处理共 60 钵, 均分为 3 组作为 3 次重复。待接穗长出 3 片新叶后, 移入光强 22 klx、光周期 12 h/12 h 的 GXZ-500D 智能光照培养箱内, 先在昼/夜温度为 20 °C/10 °C 条件下预处理 2 d, 后置于昼/夜温度为 10 °C/3 °C 条件下进行低温处理 9 d, 之后在昼/夜温度为 25 °C/15 °C 下恢复 3 d。试验过程中调查各处理嫁接苗冷害指数, 并取样测定幼苗根系及上数第 2~3 片展开叶片相关指标。

1.2 测定项目与amp;方法

冷害分级标准: 0 级, 幼苗挺拔, 无任何异常症状; 1 级, 幼苗仅基部叶片边缘有轻度的皱缩萎焉; 2 级, 幼苗半数以下叶片皱缩萎焉, 叶柄轻微下垂; 3 级, 幼苗半数以上叶片皱缩萎焉, 叶柄明显下垂; 4 级, 整株叶片皱缩萎焉, 基部叶片枯黄。冷害指数 (%) = $(1 \times N_1 + 2 \times N_2 + 3 \times N_3 + 4 \times N_4 + 0 \times N_0) / (\text{处理总株数} \times 4) \times 100$, 式中 N 为相应冷害级的苗数。

幼苗根系活力采用氯化三苯基四氮唑 (TTC) 法, 丙二醛含量采用硫代巴比妥酸比色法, 可溶性糖含量采用蒽酮比色法 (赵世杰 等, 2002) 测定, 电解质渗透率用美国产 ORION TDS 电导仪测定, 脯氨酸含量采用酸性茚三酮显色法 (李合生 等, 2000) 测定。

试验数据采用 Excel 及 DPS 软件, 依据裂区试验设计进行统计处理。

2 结果与amp;分析

2.1 低温胁迫下不同根穗组合嫁接苗冷害指数的变化

表 1 是 9 种根/穗组合番茄嫁接苗在低温胁迫与常温恢复过程中 12 种接穗 (双穗分别检测其一, 表示为 RS-R 和 RS-S) 的冷害指数。为了分析根因素和穗因素及其互作对冷害指数的影响, 分别将相同根和相同穗组合嫁接苗的冷害指数取平均数, 进行多重比较, 结果 (表 2) 表明, 根因素和穗因素对冷害指数均表现出显著影响 (根因素和穗因素的 P 值均小于 0.01), 且均以 R 作为根系 (R/RS-R、R/RS-S、R/S 和 R/S) 或作为接穗 (RS/R、R/R 和 S/R) 嫁接苗的冷害指数较低, 以 RS 为根系或接穗的次之, 以 S 为根系或接穗的较高。如低温胁迫 9 d 时, 分别以 R、RS 和 S 为根系的嫁接苗冷害指数分别为 16.00%、32.75%和 57.75%, 以 R 为根系的仅是以 S 为根系的 27.71%; 而 R、RS-R、RS-S 和 S 接穗的冷害指数分别为 27.33%、32.00%、39.00%和 43.67%, R 接穗的为 S 的 62.58%, 表明根系对嫁接苗冷害指数的影响大于接穗。根 × 穗互作的 P 值均小于 0.05, 表明二者对嫁接苗冷害指数的影响也存在显著的互作效应。

表 1 不同根或穗组合番茄嫁接苗冷害指数的变化

Table 1 Changes of chilling injury index of grafted tomato seedlings with different roots or scion combinations

%

根/穗组合 Root/scion combination	测定的 接穗 Scion	低温处理天数 (+ 恢复天数) Low temperature stress days (+ Recovery days)						
		0	1	3	6	9	9+1	9+3
RS/RS	RS-R	0	7.00 ± 2.05	6.00 ± 1.76	22.00 ± 2.47	28.00 ± 2.34	21.00 ± 1.84	14.00 ± 1.53
	RS-S	0	9.00 ± 1.06	10.00 ± 3.03	26.00 ± 1.87	38.00 ± 1.33	23.00 ± 1.68	16.00 ± 1.33
RS/R	R	0	5.00 ± 2.16	4.00 ± 2.26	19.00 ± 3.01	23.00 ± 2.27	17.00 ± 1.48	13.00 ± 1.14
RS/S	S	0	10.00 ± 1.35	12.00 ± 2.83	30.00 ± 1.66	42.00 ± 3.02	31.00 ± 1.22	17.00 ± 2.15
R/RS	RS-R	0	4.00 ± 1.27	2.00 ± 2.77	8.00 ± 3.12	13.00 ± 1.63	10.00 ± 2.04	7.00 ± 2.46
	RS-S	0	7.00 ± 2.14	6.00 ± 1.95	12.00 ± 2.83	17.00 ± 2.33	13.00 ± 2.25	10.00 ± 3.26
R/R	R	0	2.00 ± 3.15	2.00 ± 2.05	7.00 ± 1.94	12.00 ± 1.92	8.00 ± 2.46	5.00 ± 2.77
R/S	S	0	9.00 ± 2.57	7.00 ± 2.06	14.00 ± 2.64	22.00 ± 1.86	17.00 ± 2.67	12.00 ± 2.27
S/RS	RS-R	0	8.00 ± 1.83	8.00 ± 1.45	38.00 ± 2.36	55.00 ± 1.72	43.00 ± 3.17	20.00 ± 3.08
	RS-S	0	13.00 ± 2.03	15.00 ± 2.35	44.00 ± 1.75	62.00 ± 1.61	48.00 ± 2.89	23.00 ± 2.53
S/R	R	0	12.00 ± 3.05	10.00 ± 2.94	35.00 ± 3.04	47.00 ± 2.06	34.00 ± 3.09	19.00 ± 1.83
S/S	S	0	2.00 ± 1.67	15.00 ± 1.93	50.00 ± 2.05	67.00 ± 2.14	55.00 ± 1.05	28.00 ± 2.06

注: R: 耐冷番茄 '060112'; S: 冷敏感番茄 '060911'。RS-R 和 RS-S 分别代表双穗中的 R 和 S 穗。下同。

Note: R: Chilling-resistant tomato '060112'; S: Chilling-sensitive tomato cultivar '060911'. RS-R and RS-S represent the R and S scion in the double scion, respectively. The same below.

表 2 相同根或穗组合番茄嫁接苗冷害指数平均数的多重比较

Table 2 Multiple comparison of average number of chilling injury index of grafted tomato seedlings

with same roots or scion combinations

%

因子 Factor	根或穗 (组合) Root or scion (Combination)	低温处理天数 (+ 恢复天数) Low temperature stress days (+ Recovery days)						
		0	1	3	6	9	9+1	9+3
根 Root	RS (RS/RS-R, RS/RS-S, RS/R, RS/S)	0	7.75 b	8.00 b	24.25 b	32.75 b	23.00 b	15.00 b
	R (R/RS-R, R/RS-S, R/R, R/S)	0	5.50 c	4.25 c	10.25 c	16.00 c	12.00 c	8.50 c
	S (S/RS-R, S/RS-S, S/R, S/S)	0	8.75 a	12.00 a	41.75 a	57.75 a	45.00 a	22.50 a
穗 Scion	RS-R (RS/RS-R, R/RS-R, S/RS-R)	0	6.33 b	5.33 c	22.67 c	32.00 c	24.67 c	13.67 ab
	RS-S (RS/RS-S, R/RS-S, S/RS-S)	0	9.67 a	10.33 b	27.33 b	39.00 b	28.00 b	16.33 a
	R (RS/R, R/R, S/R)	0	6.33 b	5.33 c	20.33 d	27.33 d	19.67 d	12.33 b
	S (RS/S, R/S, S/S)	0	7.00 b	11.33 a	31.33 a	43.67 a	34.33 a	19.00 a
P 值	根 Root	0	0	0	0	0	0	0
P value	穗 Scion	0	0	0	0	0	0	0
	根 × 穗 Root × Scion	0	0	0	0	0.002	0	0.018

注: 表中数值后不同小写字母表示处理间差异达 0.05 显著水平。下同。

Note: Values in the table followed by different lowercase letters are significant at 0.05 level, respectively. The same below.

2.2 低温胁迫下不同根穗组合嫁接苗根系活力的变化

低温胁迫下不同处理番茄嫁接苗根系活力均不断下降, 常温恢复后又明显升高 (表 3)。如表 4 所示, 分别将相同根和相同穗组合嫁接苗的根系活力取平均值进行多重比较, 可见, 低温胁迫前, 不同处理根穗组合嫁接苗的根系活力差异不显著, 低温胁迫及常温恢复过程中则均表现出极显著差异, 且无论是作为根系还是作为接穗, 均以 R 较高, S 较低, 而 RS 双根或双穗组合居中, 但 RS 根中以 RS-R (双根系 RS 中的 R 根) 的根系活力显著高于 RS-S (双根系 RS 中的 S 根)。如低温胁迫 9 d 时, R 根系活力为 $99.91 \mu\text{g} \cdot \text{g}^{-1}$, 较 S 根高 122.12%, RS-R 根较 RS-S 根高 25.43%; 以 R 为接穗的嫁接苗根系活力较 S 穗的高 20.55%, 但增幅较 R 根系比 S 根系嫁接苗的增加幅度显著降低, 说明尽管接穗也影响根系活力, 但不及根系的作用大。除低温胁迫前根、穗对嫁接苗根系活力的交互效应不显著外, 低温胁迫及常温恢复条件下根穗间均存在显著 ($P \leq 0.05$) 或极显著 ($P \leq 0.01$)

的交互效应。

表 3 不同根或穗组合番茄嫁接苗根系活力的变化

Table 3 Changes of root activity of grafted tomato seedlings with different roots or scion combinations $\mu\text{g} \cdot \text{g}^{-1}$

根/穗组合 Root/Scion combination	测定的 根系 Root	低温处理天数 (+ 恢复天数) Low temperature stress days (+ Recovery days)						
		0	1	3	6	9	9+1	9+3
RS/RS	RS-R	239.15 ± 9.11	216.58 ± 8.61	162.16 ± 6.24	117.85 ± 5.32	71.89 ± 7.64	108.89 ± 2.14	140.83 ± 4.22
	RS-S	240.18 ± 8.64	205.81 ± 3.89	141.24 ± 9.64	100.02 ± 9.68	60.94 ± 2.14	93.83 ± 11.41	125.95 ± 2.15
R/RS	R	238.06 ± 4.58	220.47 ± 5.77	188.94 ± 7.73	136.94 ± 2.78	97.57 ± 9.71	126.53 ± 9.12	157.64 ± 8.12
S/RS	S	239.20 ± 6.63	200.98 ± 8.93	124.39 ± 3.11	80.18 ± 4.73	43.54 ± 6.32	70.64 ± 12.24	110.97 ± 8.06
RS/R	RS-R	240.04 ± 9.46	217.41 ± 2.55	170.22 ± 3.46	125.14 ± 9.94	83.12 ± 4.59	113.74 ± 9.06	145.85 ± 5.08
	RS-S	239.04 ± 7.21	207.38 ± 6.52	145.08 ± 8.11	108.76 ± 8.21	63.78 ± 8.54	99.74 ± 15.04	127.47 ± 1.14
R/R	R	238.79 ± 2.64	222.78 ± 5.58	199.90 ± 9.14	143.54 ± 1.59	110.08 ± 2.45	129.31 ± 8.14	166.91 ± 7.12
S/R	S	239.81 ± 9.85	201.87 ± 9.15	127.64 ± 9.64	84.95 ± 10.21	50.81 ± 6.50	77.03 ± 13.62	114.18 ± 3.09
RS/S	RS-R	237.94 ± 7.58	211.06 ± 7.32	151.04 ± 7.02	115.14 ± 3.14	68.87 ± 5.43	104.13 ± 8.08	133.31 ± 6.16
	RS-S	239.11 ± 7.94	205.54 ± 1.68	135.56 ± 7.61	92.08 ± 12.37	53.78 ± 7.33	85.78 ± 13.14	120.84 ± 9.28
R/S	R	240.58 ± 5.48	218.79 ± 7.16	180.54 ± 5.03	129.64 ± 6.05	92.08 ± 9.36	118.32 ± 7.02	151.89 ± 1.29
S/S	S	237.97 ± 9.05	198.34 ± 8.21	120.02 ± 9.54	77.08 ± 15.05	40.58 ± 8.40	66.17 ± 11.19	104.13 ± 9.72

表 4 相同根或穗组合番茄嫁接苗根系活力平均数的多重比较

Table 4 Multiple comparison of average number of root activity of grafted tomato seedlings with same roots or scion combinations $\mu\text{g} \cdot \text{g}^{-1}$

因子 Factor	根或穗 (组合) Root or scion (Combination)	低温处理天数 (+ 恢复天数) Low temperature stress days (+ Recovery days)						
		0	1	3	6	9	9+1	9+3
根 Root	RS-R (RS-R/RS, RS-R/R, RS-R/S)	239.04 a	215.02 a	161.14 a	119.38 a	74.63 a	108.92 b	140.00 b
	RS-S (RS-S/RS, RS-S/R, RS-S/S)	239.44 a	206.24 b	140.63 b	100.41 b	59.50 b	93.12 c	124.75 c
	R (R/RS, R/R, R/S)	239.14 a	220.68 c	189.79 b	136.71 c	99.91 c	124.72 a	158.81 a
	S (S/RS, S/R, S/S)	238.99 a	200.40 d	124.02 c	80.74 d	44.98 d	71.28 d	109.76 d
穗 Scion	RS (RS-R/RS, RS-S/RS, R/RS, S/RS)	239.15 a	210.96 e	154.18 d	108.75 e	68.48 e	99.97 b	133.85 b
	R (RS-R/R, RS-S/R, R/R, S/R)	239.42 a	212.36 f	160.71 e	115.69 e	76.95 f	104.96 a	138.60 a
	S (RS-R/S, RS-S/S, R/S, S/S)	238.90 a	208.43 g	146.79 f	103.49 f	63.83 g	93.60 c	127.54 c
P 值 P value	根 Root	0.967	0	0	0	0	0	0
	穗 Scion	0.783	0	0	0	0	0	0
	根 × 穗 Root × Scion	0.995	0	0.001	0	0	0.024	0

2.3 低温胁迫对不同根穗组合嫁接苗叶片渗透调节物质含量的影响

表 5、表 6 表明, 低温胁迫前不同处理番茄嫁接苗叶片电解质渗透率、可溶性糖及脯氨酸含量均无显著差异, 而低温胁迫则显著提高了其含量, 但 R 根或 R 穗嫁接苗叶片的脯氨酸及可溶性糖含量均显著高于 RS 及 S。如低温胁迫 9 d 时, R 穗嫁接苗叶片可溶性糖含量分别比 RS-R、RS-S、S 穗的高 3.22%、17.22%、23.90%, 脯氨酸含量分别高 3.71%、9.04%、13.66%。低温胁迫下电解质渗透率以 S 根或 S 穗处理的叶片较高, R 较低, RS-S、RS-R 居中。如低温胁迫 9 d 时, 分别以 S、RS-S、RS-R、R 为接穗的叶片电解质渗透率分别比胁迫前增加了 236.10%、222.29%、194.97%、179.89%。常温恢复下, 各处理番茄嫁接苗叶片电解质渗透率、可溶性糖及脯氨酸含量均显著下降, 且除低温胁迫前外, 根、穗对叶片电解质渗透率、可溶性糖及脯氨酸含量的影响均表现出极显著 ($P \leq 0.01$) 的互作效应。

表 5 不同根或穗组合番茄嫁接苗叶片生理特性的变化

Table 5 Changes of physiological character of leaves in grafted tomato seedlings with different roots or scion combinations

根/穗组合 Root/Scion combination	接穗 Scion	电解质渗透率/% Electrolyte permeability			可溶性糖/(mg·g ⁻¹ FW) Soluble sugar			脯氨酸/(μg·g ⁻¹ FW) Proline		
		0 d	9 d	(9+3) d	0 d	9 d	(9+3) d	0 d	9 d	(9+3) d
RS/RS	RS-R	14.49 ± 1.25	42.04 ± 1.41	26.98 ± 1.25	1.32 ± 0.22	6.97 ± 0.65	2.56 ± 0.54	115.94 ± 5.18	333.81 ± 4.23	173.22 ± 3.68
	RS-S	14.48 ± 1.75	49.02 ± 2.04	33.95 ± 0.98	1.42 ± 0.24	6.07 ± 0.88	2.36 ± 0.55	115.82 ± 3.77	313.07 ± 5.32	162.80 ± 4.55
RS/R	R	14.52 ± 2.50	41.15 ± 1.12	26.11 ± 1.98	1.31 ± 0.31	7.11 ± 0.78	2.67 ± 0.64	116.17 ± 4.12	340.75 ± 3.61	174.56 ± 4.08
RS/S	S	14.52 ± 1.25	49.76 ± 1.25	34.69 ± 2.11	1.46 ± 0.36	5.90 ± 1.01	2.20 ± 0.74	116.13 ± 6.15	305.98 ± 3.72	161.70 ± 5.15
R/RS	RS-R	14.39 ± 1.12	35.41 ± 1.22	21.65 ± 1.45	1.36 ± 0.26	8.02 ± 0.85	2.82 ± 0.71	115.15 ± 4.33	387.69 ± 3.73	191.39 ± 4.88
	RS-S	14.47 ± 2.02	39.04 ± 2.03	24.98 ± 0.87	1.27 ± 0.25	7.63 ± 1.02	2.94 ± 0.68	115.79 ± 5.13	375.55 ± 3.84	179.11 ± 5.13
R/R	R	14.53 ± 2.05	30.12 ± 1.67	18.98 ± 1.59	1.35 ± 0.11	8.43 ± 0.93	3.01 ± 0.84	116.21 ± 3.75	409.69 ± 6.33	207.24 ± 6.05
R/S	S	14.51 ± 1.55	39.87 ± 0.95	25.88 ± 1.27	1.30 ± 0.20	7.53 ± 0.69	2.74 ± 0.52	116.06 ± 6.05	364.16 ± 4.05	177.22 ± 6.03
S/RS	RS-R	14.44 ± 1.65	51.04 ± 1.87	48.27 ± 1.07	1.39 ± 0.33	4.59 ± 0.92	2.14 ± 0.74	115.51 ± 3.82	282.50 ± 6.02	159.60 ± 4.82
	RS-S	14.58 ± 1.75	51.97 ± 0.97	41.28 ± 1.05	1.42 ± 0.37	3.55 ± 1.00	2.03 ± 0.55	116.60 ± 5.66	266.30 ± 3.58	147.40 ± 4.64
S/R	R	14.37 ± 0.55	50.22 ± 1.76	39.58 ± 2.08	1.34 ± 0.32	4.69 ± 0.74	2.20 ± 0.69	114.96 ± 4.92	290.80 ± 5.22	160.71 ± 3.89
S/S	S	14.47 ± 0.85	56.03 ± 1.04	49.88 ± 0.99	1.40 ± 0.27	2.87 ± 0.67	1.97 ± 0.49	115.72 ± 4.62	246.01 ± 5.05	127.44 ± 5.26

表 6 相同根或穗组合番茄嫁接苗叶片生理特性平均数的多重比较

Table 6 Multiple analysis of average number of physiological character of leaves in grafted tomato seedlings with same roots or scion combinations

因子 Factor	根或穗(组合) Root or scion (Combination)	电解质渗透率/% Electrolyte permeability			可溶性糖/(mg·g ⁻¹ FW) Soluble sugar			脯氨酸/(μg·g ⁻¹ FW) Proline		
		0 d	9 d	(9+3) d	0 d	9 d	(9+3) d	0 d	9 d	(9+3) d
根 Root	RS (RS/RS-R, RS/RS-S, RS/R, RS/S)	14.50 a	45.49 b	30.43 b	1.37 a	6.52 b	2.45 b	116.02 a	323.40 b	168.07 b
	R (R/RS-R, R/RS-S, R/R, R/S)	14.48 a	36.11 c	22.87 c	1.32 a	7.90 a	2.88 a	115.80 a	384.27 a	188.74 a
	S (S/RS-R, S/RS-S, S/R, S/S)	14.46 a	52.32 a	44.75 a	1.39 a	3.93 c	2.08 c	115.70 a	271.40 c	148.79 c
穗 Scion	RS-R (RS/RS-R, R/RS-R, S/RS-R)	14.44 a	42.83 c	32.30 b	1.35 a	6.53 a	2.51 b	115.53 a	334.67 b	174.74 b
	RS-S (RS/RS-S, R/RS-S, S/RS-S)	14.51 a	46.68 b	33.40 b	1.37 a	5.75 b	2.44 c	116.07 a	318.31 c	163.10 c
	R (RS/R, R/R, S/R)	14.47 a	40.50 d	28.22 c	1.33 a	6.74 a	2.63 a	115.78 a	347.08 a	180.84 a
	S (RS/S, R/S, S/S)	14.50 a	48.55 a	36.82 a	1.38 a	5.44 b	2.30 d	115.97 a	305.38 d	155.45 d
P 值	根 Root	0.880	0	0	0.482	0	0	0.928	0	0
P value	穗 Scion	0.969	0	0.001	0.866	0	0	0.947	0	0
	根 × 穗 Root × Scion	0.975	0	0	0.780	0.003	0	0.975	0	0

2.4 低温胁迫对不同根穗组合嫁接苗根系渗透调节物质含量的影响

低温胁迫前不同处理番茄嫁接苗根系电解质渗透率、可溶性糖及脯氨酸含量无显著差异，低温胁迫下均显著升高，常温恢复后又显著下降，且以 R 根或 R 穗嫁接苗根系的电解质渗透率较低，可溶性糖及脯氨酸含量较高，S 根或 S 穗嫁接苗则刚好相反，RS 根或 RS 穗嫁接苗居中，但 RS-R 根中的电解质渗透率显著低于 RS-S，而可溶性糖及脯氨酸含量则相反（表 7，表 8）。如低温胁迫 9 d 时，RS-R 根的电解质渗透率比 RS-S 低 11.42%，而可溶性糖及脯氨酸含量分别高 18.08%、5.49%，且除低温胁迫前外，根和穗之间均存在极显著 ($P \leq 0.01$) 的互作效应。

表 7 不同根或穗组合番茄嫁接苗根系生理特性的变化

Table 7 Changes of physiological character of roots in grafted tomato seedlings with different roots or scion combinations

根/穗组合 Root/Scion combination	根系 Root	电解质渗透率/%			可溶性糖/(mg·g ⁻¹ FW)			脯氨酸/(μg·g ⁻¹ FW)		
		Electrolyte permeability			Soluble sugar			Proline		
		0 d	9 d	(9+3) d	0 d	9 d	(9+3) d	0 d	9 d	(9+3) d
RS/RS	RS-R	21.84±2.14	54.72±1.35	39.82±2.04	0.81±0.17	4.09±0.76	2.67±0.63	59.84±6.24	232.03±4.11	121.81±4.91
	RS-S	22.75±1.99	61.23±2.02	43.59±1.83	0.82±0.11	3.46±0.71	2.30±0.32	59.75±7.13	227.46±6.53	105.43±6.32
R/RS	R	22.91±3.02	49.04±1.28	31.56±1.88	0.81±0.20	4.67±0.51	3.01±0.52	59.91±5.96	272.53±3.86	129.32±5.24
S/RS	S	21.99±1.84	69.25±3.01	49.63±2.79	0.82±0.16	3.01±0.63	2.13±0.69	58.99±6.57	191.63±5.25	102.53±5.66
RS/R	RS-R	22.19±3.08	52.24±2.09	37.54±3.03	0.78±0.19	4.21±0.42	2.80±0.44	59.19±4.86	240.79±6.33	123.66±4.81
	RS-S	22.54±2.55	60.14±2.23	42.63±2.15	0.80±0.23	3.56±0.55	2.43±0.36	60.54±5.11	228.33±5.46	110.83±5.65
R/R	R	21.48±3.07	41.35±1.63	28.76±3.01	0.77±0.14	4.96±0.62	3.24±0.39	58.48±4.71	291.83±6.57	136.91±5.83
S/R	S	22.15±3.02	67.43±3.05	48.09±2.83	0.77±0.15	3.12±0.76	2.16±0.47	59.15±5.81	198.45±4.97	103.54±6.43
RS/S	RS-R	21.65±2.25	55.96±2.43	40.55±2.57	0.81±0.09	3.85±0.33	2.56±0.58	58.65±6.55	230.15±5.15	119.85±6.45
	RS-S	23.07±2.89	62.57±2.45	44.77±2.26	0.79±0.12	3.27±0.59	2.27±0.72	60.07±7.05	210.57±6.33	105.75±4.54
R/S	R	21.74±3.03	50.18±1.81	32.87±3.09	0.80±0.21	4.51±0.64	2.92±0.63	58.74±6.17	261.88±4.63	127.24±5.53
S/S	S	22.36±2.53	78.03±1.78	57.76±1.99	0.80±0.10	2.44±0.73	1.91±0.71	59.36±5.57	153.26±5.26	85.41±6.41

表 8 相同根或穗组合番茄嫁接苗根系生理特性平均数的多重比较

Table 8 Multiple analysis of average number of physiological character of roots in grafted tomato seedlings with same roots or scion combinations

因子 Factor	根或穗(组合) Root or scion (Combination)	电解质渗透率/%			可溶性糖/(mg·g ⁻¹ FW)			脯氨酸/(μg·g ⁻¹ FW)		
		Electrolyte permeability			Soluble sugar			Proline		
		0 d	9 d	(9+3) d	0 d	9 d	(9+3) d	0 d	9 d	(9+3) d
根 Root	RS-R (RS-R/RS, RS-R/R, RS-R/S)	21.89 a	54.31 c	39.30 c	0.80 a	4.05 b	2.68 b	59.23 a	234.32 b	121.77 b
	RS-S (RS-S/RS, RS-S/R, RS-S/S)	22.79 a	61.31 b	43.66 b	0.80 a	3.43 c	2.33 c	60.12 a	222.12 c	107.34 c
	R (R/RS, R/R, R/S)	22.04 a	46.86 d	31.06 d	0.79 a	4.72 a	3.06 a	59.04 a	275.41 a	131.16 a
	S (S/RS, S/R, S/S)	22.17 a	71.57 a	51.83 a	0.79 a	2.86 d	2.07 d	59.17 a	181.11 d	97.16 d
穗 Scion	RS (RS-R/RS, RS-S/RS, R/RS, S/RS)	22.37 a	58.56 b	41.15 b	0.81 a	3.81 b	2.53 b	59.62 a	230.91 b	114.77 b
P 值 P value	根 Root	0.641	0	0	0.999	0	0	0.641	0	0
	穗 Scion	0.979	0	0	0.786	0	0	0.979	0	0
	根 × 穗 Root × Scion	0.992	0	0	1.000	0	0.005	0.992	0	0.002

3 讨论

低温引发叶片皱缩、萎蔫等症状是植物冷害最直观的表现(田丹青等, 2011)。Cao等(2011)研究表明, 低温能够显著抑制油棕幼苗的生长, 其叶片冷害指数随低温胁迫时间的延长而显著增加。本研究中, 低温胁迫3 d时, S为根或穗的嫁接苗冷害指数较1 d时显著升高, 而R为根或穗的嫁接苗则在1~3 d内有所下降, 这可能是初期的低温胁迫对耐冷性较强的R嫁接苗起到了一定的锻炼作用, 而冷敏感的S则受到了低温损伤。但随着低温处理时间的延长, 冷害胁迫逐步加重, 各处理嫁接苗的冷害指数均持续增加, 但仍以R为根或穗的嫁接苗冷害指数显著低于S为根或穗的嫁接苗。

前人研究表明, 嫁接可有效增强西瓜、辣椒植株的根系活力和细胞膜的稳定性, 从而提高其耐冷性(刘慧英等, 2003; 王洪涛等, 2010)。本研究中, 不仅耐冷性强的根系可增强细胞膜的稳定性, 减少溶质的外流, 耐冷性强的接穗也有相同的效果, 表明耐冷性强的根、穗均可提高嫁接苗的

耐冷性, 由此进一步证实了砧木与接穗双方的抗冷特性是获得嫁接苗抗冷性的关键这一观点(于贤昌等, 1998)。但耐冷性弱的根、穗则可能导致嫁接苗细胞膜稳定性的下降, 致使溶质外流增多, 表明其对嫁接苗的耐冷性产生了负效应, 与此相似, 于贤昌等(1998)的研究也证实, 选用较南瓜砧木耐冷性低的黄瓜品种作为接穗, 在一定程度上可削弱砧木根系的抗冷性。不仅如此, 本研究中不同根系或接穗组合嫁接苗中均以“R”的冷害指数及电解质渗透率较小, 以“S”较大, 双根或双穗组合“RS”居中, 且“RS”根或穗中又以“RS-R”的细胞膜稳定性显著高于“RS-S”, 表明根、穗对嫁接苗耐冷性存在显著的互作效应。

细胞膜作为植物冷害的原初反应部位, 在低温胁迫下易由液晶状态变成凝结状态, 从而引起细胞膜的损伤及膜酶功能的改变(Thomashow, 1999), 但低温胁迫下植物体可通过产生渗透调节物质来调控相应的生理代谢途径, 以此降低或消除对植物造成的伤害(徐澜等, 2015; 薄晓培等, 2016), 而游离脯氨酸和可溶性糖是植物体内与抗逆关系最为密切的渗透调节物质(李阳阳等, 2016; 姚海梅等, 2016)。本试验低温胁迫期间, 具S接穗或根系的嫁接苗RS/R、R/RS、S/RS、RS/S中R叶片及根系的可溶性糖及脯氨酸含量均低于R/R, 表明耐冷性弱的S接穗或根系均起到了降低R抗冷性的作用; 而具R接穗或根系的嫁接苗RS/R、R/RS、S/RS、RS/S中S叶片及根系的可溶性糖及脯氨酸含量则均高于S/S, 表明耐冷性强的R接穗或根系均提高了S的抗冷性。但由于RS/RS中的R与S叶片和根系的可溶性糖及脯氨酸含量均相应高于S/RS, 而低于R/RS, 表明根系在增强嫁接苗耐冷性中的作用大于接穗。

低温能显著抑制作物根系的生长, 破坏根系膜系统, 致使细胞膜透性的增加(罗宁等, 2014), 根系活力下降(Li et al., 2008), 严重阻碍了根系对养分的吸收和转运(吕德国等, 2010), 最终导致植株生长发育不良。高青海等(2006)的研究表明, 利用抗性砧木进行嫁接可显著缓解低温胁迫对茄子根系的损伤程度。本试验中, 不仅R/S组合嫁接苗中R的根系活力显著高于S/S组合中的S根系, 且S/R组合中S的根系活力也显著高于S/S组合, 表明耐冷性强的根系或接穗均能显著增强嫁接苗的根系活力, 提高其耐冷性。而R/S及S/R组合嫁接苗中R或S的根系活力均显著低于R/R组合, 表明耐冷性弱的根、穗均可导致嫁接苗根系活力的下降, 从而削弱嫁接苗的耐冷性。本研究中还发现, RS/RS既有R根系又有S根系, 其双根系吸收能力应强于R/RS和S/RS, 但RS/RS在低温胁迫下的根系活力仅强于S/RS, 而不及R/RS, 这可能是由于RS/RS组合中S根、穗在低温胁迫过程中产生了不耐低温的信号, 如植物激素(Aloni et al., 2010)及特定的RNA分子(Harada, 2010; 孙敬爽等, 2014)等, 削弱了嫁接苗中R的抗冷性, 其具体作用机制还有待进一步研究。

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