

5个砧木苹果枝条的抗寒性评价

刘兴禄¹, 王红平^{1,2a}, 孙文泰¹, 董铁¹, 牛军强¹, 马明^{1*}

(¹甘肃省农业科学院林果花卉研究所, 兰州 730070; ²张掖市林业科学研究院, 甘肃张掖 734000)

摘要:【目的】对不同砧木的长富2号(Nagano Fuji No.2)苹果枝条进行抗寒性综合评价,旨在筛选能提高长富2号苹果抗寒性的优良砧木,为陇东地区长富2号苹果抗寒栽培和砧木引进提供理论依据。【方法】以SH1、Y-1、B9、T337和M26砧木嫁接的1年生深度休眠期苹果枝条为试材,分别在-15、-20、-25、-30、-35、-40℃的低温处理12h,测定相对电导率(REC)、丙二醛(MDA)、可溶性糖(SS)、游离脯氨酸(Pro)含量,以及过氧化物酶(POD)、超氧化物歧化酶(SOD)活性等生理指标。利用电导法结合Logistic方程和隶属函数法综合评价5个砧木苹果枝条的抗寒性。【结果】随着温度的降低,5个砧木苹果枝条的相对电导率逐渐升高,呈“S”形变化曲线;丙二醛、可溶性糖和游离脯氨酸在低温半致死温度附近出现突然跃变的现象;抗寒性强的砧木品种能保持较高的酶活性。【结论】5个砧木品种的耐寒性由强到弱依次为B9(-40.1℃)>SH1(-36.0℃)>Y-1(-32.7℃)>M26(-31.3℃)>T337(-23.4℃)。

关键词: 苹果砧木; 苹果枝条; 抗寒性; 低温胁迫; 低温半致死温度; 隶属函数法; 生理变化

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Cold resistance evaluation of the shoots of 5 apple rootstocks

LIU Xinglu¹, WANG Hongping^{1,2a}, SUN Wentai¹, DONG Tie¹, NIU Junqiang¹, MA Ming^{1*}

(¹Institute of Fruit and Flower, Gansu Academy of Agricultural Sciences, Lanzhou 730070, Gansu, China; ²Zhangye Forestry Science Academy, Zhangye 734000, Gansu, China)

Abstract: 【Objective】The cold resistance of the hardwoods of different root-stocks was evaluated comprehensively in order to select rootstocks that improve the cold resistance of ‘Nagano Fuji No.2’ apple, which is susceptible to cold injury in winter. Cold injury usually causes yield reduction and even crop failure, which is disastrous for farmers and seriously affects the development of apple industry. The existing studies mainly focus on frozen injury in apple in winter, but few reports concern about the mechanisms of response to cold temperatures. In this study, we used the membership function and the semi-lethal temperature(LT₅₀) to analyze changes in antioxidant enzymes and osmotic regulators in apple under cold stress in order to provide a theoretical reference for cultivar introduction, cold resistance breeding and cultivation. 【Methods】One-year-old hardwoods of five apple rootstocks including SH1, Y-1, B9, T337 and M26 were placed in incubators for low temperature treatment. The experiment set six temperature treatments including exposure of the hardwoods to room temperature (CK), -15 °C, -25 °C, -30 °C, -35 °C and -40 °C under darkness for 12 h. Each treatment composed of three replicates. Samples were taken to determine the membrane leakage reflected by relative electric conductivity (REC), or frozen in liquid nitrogen then stored at -80 °C for analyses of malondialdehyde (MDA), contents of soluble sugars and free proline and the enzymatic activities of peroxidase (POD) and superoxide dismutase (SOD). 【Results】The REC value of the hardwoods of the five cultivars increased following an S curve

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作者简介: 刘兴禄, 男, 农艺师, 研究方向为果树栽培技术。Tel: 13619316269, E-mail: 460836078@qq.com。a为共同第一作者。

*通信作者 Author for correspondence. Tel: 13893685370, E-mail: maming65118@163.com

with the decrease in temperature. The rapid increase in REC in different cultivars occurred at different temperatures. The REC values of T337 and M26 increased significantly when temperature was below $-25\text{ }^{\circ}\text{C}$; SH1 exposed to cold stress for 12 h behaved similar to Y-1. When temperature was lower than $-25\text{ }^{\circ}\text{C}$, the REC values of SH1 and Y-1 significantly rose. Regressed logistic equations between temperature and REC values in the five cultivars exposed to the cold temperatures for 12 h were established. LT_{50} value was calculated from the established equations, which were used to measure the cold resistance of apple. The cold resistance based on LT_{50} in the five rootstock cultivars was in the order of $B9 > SH1 > Y-1 > M26 > T337$. MDA content in all the cultivars was higher than in the control. MDA content in all the cultivars gradually increased with the decrease in temperature, and reached the highest value at $-35\text{ }^{\circ}\text{C}$. The highest MDA was found in SH1 and the lowest in Y-1. MDA in T337 was higher than in the other cultivars. B9 had the lowest MDA content among all the cultivars. The range of increase in MDA was the largest in T337 and lowest in B9 and SH1. As the temperature became lower, SOD and POD activities showed different change patterns in different cultivars. SOD activity in SH1 and Y-1 rose first and then declined. We set that under low temperature stress of $CK - 40\text{ }^{\circ}\text{C}$, SOD curves of B9 and SH1 changed similarly, both of which were "M" type. The SOD activity of SH1 showed "N" type under low temperature stress, reached the lowest peak at a certain inflection point of low temperature stress, and then continued to increase. Y-1 maintained a significantly higher SOD activity than other cultivars at all the low temperatures, followed by SH1 and B9. Low temperature stress increased SOD activity. Compared with the control group, the increasing range of T337 was larger, while those of SH1 and Y-1 were smaller than the others. POD activity in B9 and T337 increased in the early period and then decreased. The enzyme activity in Y-1 and SH1 displayed a trend of decreasing-increasing-decreasing, but its change was slight. POD activity in M26 was significantly higher than that in the other cultivars. In all the temperature treatments in M26, POD activity was lower than in the other cultivars. POD activity in the five rootstock cultivars exposed to the low temperatures was higher than in the control. POD activity significantly rose when temperature dropped to below $-30\text{ }^{\circ}\text{C}$, and the rising range was the largest in T337 and smallest in M26. CAT activity was higher in cold stressed groups than in the control. SH1 and Y-1 had their peak CAT activities at $-25\text{ }^{\circ}\text{C}$ and T337 and M26 at $-35\text{ }^{\circ}\text{C}$. Seven treatments in B9 were lowest among all the cultivars. Same to POD, the largest and lowest increasing range was found in T337 and M26, respectively. **【Conclusion】** REC, MDA content, soluble sugar, and SOD and POD activities were increased by cold stresses. With temperature drop, REC and MDA content in the five rootstock cultivars increased; the change patterns of SOD and POD activities differed among cultivars. The LT_{50} and the changes in protective enzyme activities showed that cold resistance in the cultivars was in the order of $B9 > SH1 > Y-1 > M26 > T337$.

Key words: Apple rootstock; Apple branches; Cold resistance; Low temperature stress; Semi-lethal-low temperature; Membership function method; Physiological change

陇东地区是甘肃苹果生产的主要地区,也是国内重要的苹果优势主产区之一^[1],但该地区的严寒气候已成为制约苹果成规模生产的重要生态因子之一^[2]。近年来,该地区春季气温回升快,冷暖变化剧烈,加之晚霜冻等不稳定的天气导致苹果产量出现明显的下降。仅2011年期间,甘肃省因低温等天气灾害造成的经济林果受灾面积高达26.61万 hm^2 ,直接经济损失逾14.03亿元^[3]。因此,对苹果的抗寒性

进行鉴定评价显得尤为重要和迫切^[2-3]。王依等^[4]和刘贝贝等^[5]分别在葡萄和石榴枝条中研究发现,植物遭受低温胁迫,会使各组织器官中的可溶性糖、可溶性蛋白、游离脯氨酸和丙二醛含量逐渐升高,而不同品种在各温度处理下升降的速度和幅度差异明显。众多学者以相对电导率(Relative electrical conductivity, REC)以及超氧化物歧化酶(Superoxide dismutase, SOD)、抗坏血酸过氧化物酶(Ascorbate

peroxidase, APX)、过氧化氢酶(Catalase, CAT)活性等生理指标来评价葡萄^[6]、早熟禾^[7]、油菜^[8]和石榴^[9]的抗寒性。吕优伟等^[10]用电导法结合隶属函数法对9种不同生境的早熟禾属植物的抗寒性进行了评价,结果表明,抗寒性强的品种电导率上升幅度低于抗寒性弱的品种,恰好与隶属函数法的评价结果完全一致。于庆帆等^[11]对伊犁地区树上干杏品种进行了抗寒性评价,得出相似的结果。迄今为止,电导法结合隶属函数法广泛应运于枇杷、石榴、枸杞、核桃、葡萄等耐寒性评价及种质筛选,棉花幼苗的耐酸性评价,小麦拔节期的耐寒性评价,种子萌发期的抗旱性评价^[12-19]。但是用任何一种单一的形态或生理指标都很难客观地比较抗寒性的强弱。多元统计方法中的隶属函数法可将多种指标综合起来,以比较品种间的抗寒性差异。前人根据上述评价方法,在草莓^[20]、杏^[21]、葡萄^[22]的抗寒性综合评价中已有应用,电导法协同 Logistic 回归方程计算植物组织的半致死温度,比较多种植物的抗寒性,并取得良好效果,尤其是比较苹果品种的抗寒性应用较广^[23-27]。但是有关利用隶属函数法结合电导法评价苹果砧木抗寒性的报道颇少。笔者在本研究中以 SH1、Y-1、B9、T337 和 M26 为材料,采用隶属函数法结合电导法对 LT₅₀和低温胁迫下的生理生化物质产生的抗寒机制应答进行研究,旨在对苹果砧木品种的抗寒性进行评价,提出鉴定苹果砧木抗寒性的方法,为抗寒性强的苹果砧木品种选育提供依据。

1 材料和方法

1.1 材料采集

2018年12月12日于甘肃省静宁县国家苹果综合试验站,采集露地栽培管理一致、长势良好、均匀一致的1年生长富2号枝条,各砧木枝条分别采集70枝,长度截留约为60 cm,粗度约为0.75 cm,供试苹果砧木分别为SH1、Y-1、B9、T337和M26。

1.2 材料处理

将采集来的枝条依次用自来水、蒸馏水和重蒸馏水冲洗2遍,用干净细纱布擦干后,石蜡封闭枝条两端的剪口。每种砧木枝条分成7组,每组10条,留下其中一组,在室温下测定作为对照(CK),其余枝条用干净细纱布包裹后装入塑料袋并标好标签,分别在-15、-20、-25、-30、-35、-40℃低温下进行冷冻处理,冷冻时温度下降和解冻时的温度回升幅度都

为4℃·h⁻¹,到达目标温度后持续12 h,然后解冻至室温放置12 h。冷冻前后冰箱温度均保持在固定温度4℃,采用LRH-250CB低温冰箱,控温精度±1℃,然后进行相关指标的测定。

1.3 测定指标与方法

相对电导率用 DDS-11A 型电导仪测定^[28];丙二醛含量采用硫代巴比妥酸法测定^[28];可溶性糖含量采用蒽酮乙酸乙酯法测定^[28];脯氨酸含量采用茚三酮比色法测定^[29];过氧化物酶(POD)活性采用愈创木酚比色法^[29]测定;超氧化物歧化酶(SOD)活性采用氮蓝唑(NBT)还原法^[29]测定。运用 Logistic 方程计算低温半致死温度(LT₅₀)^[30]。

1.4 抗寒性评判

应用隶属函数法综合评判抗寒性^[31-35]。

1.5 统计分析

采用 Microsoft Excel 2010 整理数据并作图,用 SPSS 16.0 软件进行 Logistic 方程拟合和差异显著性分析。

2 结果与分析

2.1 低温胁迫下相对电导率的变化

相对电导率达到50%时的温度可以作为枝条的半致死温度^[28]。表1所示,SH1、Y-1、B9、T337和M26在-35、-35、-40、-25、-30℃的相对电导率分别为55.86%、60.94%、64.08%、52.48%和65.38%,均超过了50%(低温半致死拐点温度LT₅₀),这说明SH1、Y-1、B9、T337、M26的半致死温度分别在-35、-35、-40、-25、-30℃附近。为准确判断5种苹果砧木枝条的低温半致死拐点温度LT₅₀,利用相对电导率结合Lo-

表1 不同低温处理后5个苹果砧木枝条相对电导率的变化

Table 1 Changes in relative electrical conductivity of five apple rootstock hardwoods treated with different low temperatures %

品种	不同低温 Different low temperatures						
Cultivar	CK	-15℃	-20℃	-25℃	-30℃	-35℃	-40℃
SH1	16.46 b	24.38 b	30.99 c	41.90 ab	47.49 c	55.86 c	77.11 ab
Y-1	16.75 b	23.77 b	35.73 b	39.99 c	48.44 b	60.94 b	72.19 b
B9	13.38 a	25.26 a	32.75 c	37.38 c	44.31 d	48.83 d	64.08 b
T337	22.65 b	30.48 b	40.34 a	52.48 a	72.42 a	78.15 ab	80.48 a
M26	18.71 a	27.56 a	41.33 a	43.22 bc	65.38 ab	71.56 a	77.81 ab

注:不同小写字母表示 $p < 0.05$ 差异显著水平。

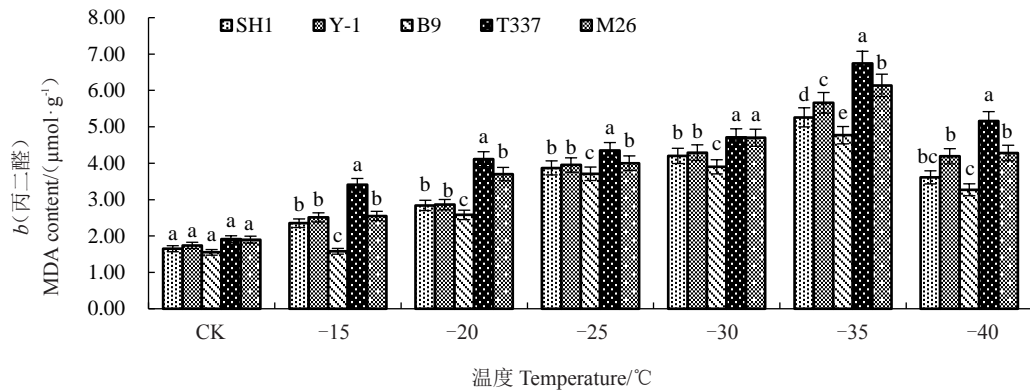
Note: Different small letters indicate significant difference ($p < 0.05$).

gistic 方程对各枝条的重要拐点温度进行拟合(R^2 均大于0.990)。结果表明:SH1、Y-1、B9、T337和M26的组织损伤起始温度分别为-9.28、-10.42、-15.14、-13.62、-18.40℃;组织细胞膜接近全透性时的温度分别为-51.25、-48.94、-58.55、-42.64、-47.60℃;组织细胞的半致死温度分别为-36.04、-32.76、-40.14、-23.45、-31.36℃。

2.2 低温胁迫下丙二醛含量的变化

由图1所示,随着低温胁迫的加剧,各供试砧木枝条的丙二醛逐渐升高且在低温半致死温度附近突然跃变而后出现不同程度的下降,且各低温处理均高于对照。其中,在CK~-15℃低温处理区间内,各供试品种枝条MDA含量缓慢升高;T337和M26枝条的MDA含量在-15~-20℃温度处理下急剧升

高;SH1和Y-1枝条的MDA含量在-25~-30℃温度处理下升高较为平缓,但在-30~-35℃温度处理下,SH1、Y-1、B9、T337和M26枝条的MDA含量迅速升高。B9的MDA含量较其他品种相比处于较低水平,SH1、Y-1、M26的MDA含量居中,而T337的MDA含量一直处于较高水平,且显著高于其他品种($p < 0.05$);在-35℃时,各供试砧木的丙二醛含量均达到最大值且差异显著($p < 0.05$),分别为5.26、5.66、4.77、6.74、6.14 $\mu\text{mol} \cdot \text{g}^{-1}$;在-40℃时,与对照相比,各供试砧木枝条的MDA含量开始下降,下降幅度分别达45.71%、35.08%、45.87%、30.62%和43.46%。在-40℃时,各供试砧木枝条的丙二醛含量分别是各自起始温度的2.19、2.41、2.11、2.70、2.52倍。



不同小写字母表示不同品种间差异显著($p < 0.05$)。下同。

Different small letters represent significant difference among different varieties ($p < 0.05$). The same below.

图1 低温胁迫下5个苹果砧木枝条丙二醛含量的变化

Fig. 1 Changes in malondialdehyde content in five apple rootstocks under low temperature stress

2.3 低温胁迫下可溶性糖含量的变化

由图2所示,抗寒性强的苹果砧木枝条能保持较高的可溶性糖含量。其中,在CK~-15℃低温处理区间内,各供试品种枝条可溶性糖含量缓慢升高;T337和M26枝条的可溶性糖含量在-15~-20℃温度处理下急剧升高;SH1和Y-1枝条的可溶性糖含量在-25~-30℃温度处理下升高较为平缓,但在-30~-35℃温度处理下,SH1、Y-1、B9、T337和M26枝条的可溶性糖含量迅速升高。在-35℃时,各供试砧木的可溶性糖含量达到最大值且差异显著($p < 0.05$),分别为7.28%、5.96%、8.54%、5.00%和4.34%。B9的可溶性糖含量较其他品种相比处于较低水平,SH1和Y-1的可溶性糖含量居中,而T337和

M26的可溶性糖含量始终保持较低水平,且显著低于其他品种($p < 0.05$);在-40℃时,各供试砧木枝条的可溶性糖含量开始下降且此时的可溶性糖含量分别是各自起始温度的2.99、2.69、3.35、3.20、2.85倍。

2.4 低温胁迫下游离脯氨酸含量的变化

由图3可以看出:随着温度的降低游离脯氨酸含量整体呈上升趋势,从胁迫初期(-15~-20℃)到胁迫中期(-25~-30℃)游离脯氨酸含量上升幅度明显加快,从胁迫中期(-25~-30℃)到胁迫末期(-35~-40℃)虽然游离脯氨酸含量仍表现增加趋势,但增加幅度开始减缓。在-40℃时,各供试砧木枝条的游离脯氨酸含量分别是各自起始温度的2.31、4.95、5.57、8.79、4.15倍。

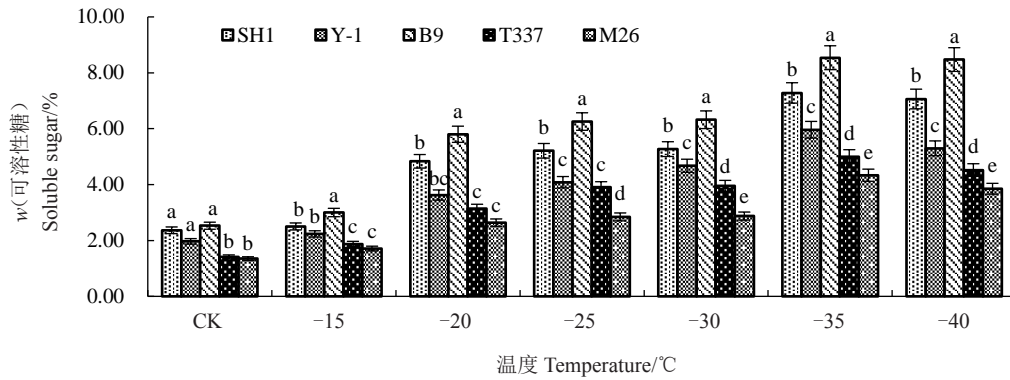


图 2 低温胁迫下 5 个砧木苹果枝条可溶性糖含量的变化

Fig. 2 Changes in soluble sugar content in five apple rootstock hardwoods under low temperature stress

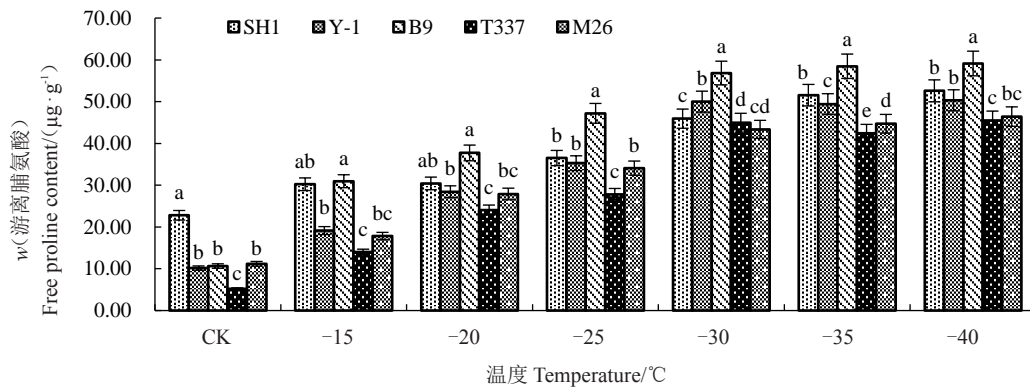


图 3 低温胁迫下 5 个砧木苹果枝条游离脯氨酸含量的变化

Fig. 3 Changes in free proline content in the hardwoods of five apple rootstocks under low temperature stress

2.5 低温胁迫下超氧化物歧化酶活性的变化

由图 4 所示,超氧化物歧化酶的活性变化趋势是随温度的降低而呈现先升高后降低的趋势,当温度降低到一定程度时,超氧化物歧化酶活性开始下降。在-40 °C 时,所有供试砧木的超氧化物歧化酶活性均呈现下降趋势,说明这种保护能力开始变弱。5 个苹果砧木的超氧化物歧化酶活性达到最高

值时由高到低依次为 B9(339.95 U·min⁻¹·g⁻¹)、SH1(214.68 U·min⁻¹·g⁻¹)、M26(214.18 U·min⁻¹·g⁻¹)、Y-1(202.72 U·min⁻¹·g⁻¹)和 T337(128.05 U·min⁻¹·g⁻¹)。与对照(CK)相比,5 个苹果砧木的超氧化物歧化酶活性达到最大值时的增量由多到少依次为 B9(218.32 U·min⁻¹·g⁻¹)、M26(141.46 U·min⁻¹·g⁻¹)、Y-1(119.99 U·min⁻¹·g⁻¹)、SH1(114.21 U·min⁻¹·g⁻¹)和

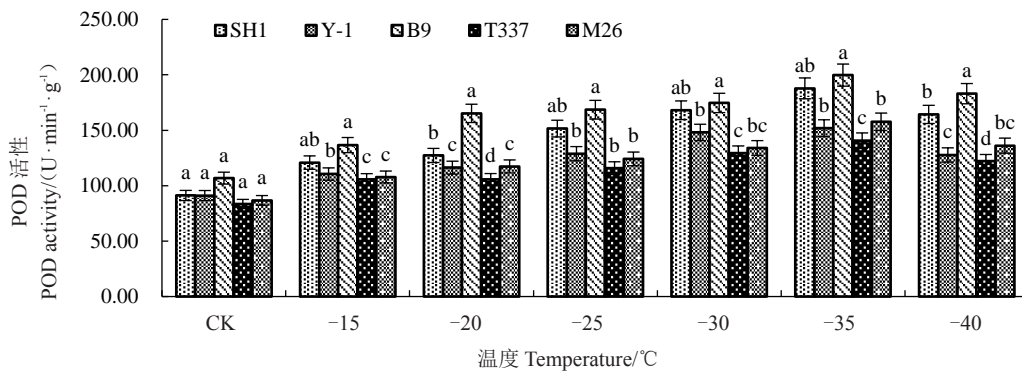


图 4 低温胁迫下 5 个砧木苹果枝条超氧化物歧化酶活性的变化

Fig. 4 Changes in peroxidase activity in five apple rootstocks under low temperature stress

T337(65.27 U·min⁻¹·g⁻¹)。在-40℃时,各供试砧木枝条的超氧化物歧化酶活性分别是各自起始温度的1.06、1.06、1.53、0.76、0.99倍。

2.6 低温胁迫下过氧化物歧化酶活性的变化

由图5所示,过氧化物歧化酶活性出现明显的先上升后下降的变化规律且不同砧木在快速上升期

间对应的胁迫温度区间明显不同。5个苹果砧木枝条的过氧化物歧化酶活性达到最高峰时由高到低依次为B9(199.77 U·g⁻¹)、SH1(187.77 U·g⁻¹)、M26(157.65 U·g⁻¹)、Y-1(151.86 U·g⁻¹)和T337(140.54 U·g⁻¹)。在-40℃时,各供试砧木枝条的过氧化物歧化酶活性分别是各自起始对照温度的1.80、1.40、

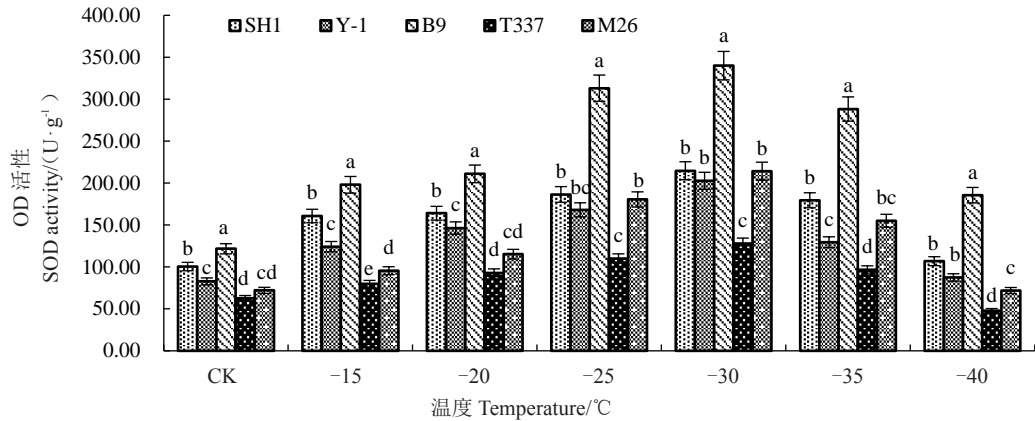


图5 低温胁迫下5个砧木苹果枝条过氧化物歧化酶活性的变化

Fig. 5 Changes in superoxide dismutase activity under low temperature stress

1.71、1.46、1.57倍。

2.7 隶属函数法综合评价抗寒性

鉴于植物抗寒性是由多种数量性状和质量遗传基因等综合作用的累加结果,并受到多重因素的影响和制约,孤立地用某单一指标评价植物的抗寒性不具有代表性。因此,采用隶属函数综合多个指标评价植物的抗寒性较为可靠。撒俊逸等^[29]运用隶属函数法评价了库尔勒香梨枝条的抗寒性发现,平均隶属值越大,抗寒性越强,反之,抗寒性越弱。表2所示:5个苹果砧木枝条的平均隶属度为0.450 4~0.692 4,B9的平均隶属度最高(0.692 4),SH1的平均隶属度次之(0.630 6),Y-1和M26的平均隶属度居中(0.483 9~0.544 9),T337的平均隶属度最低(0.450 4)。由此可见,5个苹果砧木的抗寒性由强到弱依次为B9>SH1>Y-1>M26>T337,这与低温半致死温度的验证结果一致。参照刘君等^[30]的方法,按照苗木的受冻级别可将SH1、Y-1、B9、T337和M26分别分为I、I、I、III、II级(表2)。

表2 不同苹果砧木枝条的抗寒性综合评价

Table 2 Comprehensive evaluation of cold resistance of different apple rootstocks

指标 Index	SH1	Y-1	B9	T337	M26
相对电导率 Relative conductivity	0.615 1	0.480 6	0.744 8	0.226 4	0.376 5
丙二醛含量 Malonadehyde content	0.644 1	0.605 0	0.710 7	0.462 2	0.548 0
可溶性糖含量 Soluble sugar content	0.596 9	0.471 0	0.444 1	0.288 4	0.185 6
游离脯氨酸含量 Free proline content	0.619 4	0.546 9	0.701 1	0.444 1	0.501 2
过氧化物歧化酶活性 POD activity	0.380 1	0.296 1	0.646 6	0.138 2	0.278 2
超氧化物歧化酶活性 SOD activity	0.521 0	0.496 0	0.625 1	0.606 2	0.663 6
平均隶属度 Mean membership	0.630 6	0.544 9	0.792 4	0.450 4	0.483 9
位次 Rank	2	3	1	5	4
受冻级别 Cold level	I	I	I	III	II

3 讨论

3.1 低温胁迫与相对电导率之间的关系

植物膜系统是植物受低温伤害的原发部位,其稳定性对于植物抵御低温逆境具有重要意义^[31]。相

对电导率的变化可反映细胞膜透性的改变,因此常作为评定植物细胞膜损坏程度的重要参考指标^[32]。前人研究表明,抗寒性强的植物低温胁迫下植物膜系统稳定性较好,相对电导率较小;反之,植物膜系统稳定性较差,相对电导率较大^[33]。本研究表明,随着处理温度的降低,5个供试苹果砧木枝条的相对

电导率逐渐升高,呈近似“S”形变化曲线。运用电导法配以Logistic方程计算植物的低温半致死温度,比较植物间的抗寒性差异,已在农作物牧草^[34]、辣椒^[35],木兰^[36]和园艺作物葡萄^[37]、库尔勒香梨^[38]、扁桃^[39]和杧果^[40]中得到广泛应用,并取得良好的效果。根据低温半致死温度的高低,推断出5个苹果砧木枝条的抗寒性由强到弱依次为B9>SH1>Y-1>M26>T337。甘肃陇东地区年平均气温9.5℃,1月份最冷,平均气温为-8.5℃,平均最低气温-13.2℃,极端最低气温在-28℃以下。按本试验结果可判断5种苹果砧木均可在陇东地区正常自然越冬,然而事实上陇东地区露地栽培苹果砧木仍表现出干枯、抽条冻害现象。因此,笔者推测引起陇东地区苹果砧木发生抽条伤害不仅与当年低温有关,还与当年降雪覆盖量和降雪持续时间等息息相关。因此在生产中为防止树木冻害,可考虑在定植行间浇湿井水(温水)和铺设地膜等措施来提高地温,以打破根系的休眠,促进对水分的吸收。

3.2 低温胁迫与渗透调节物质之间的关系

植物在冷胁迫过程中,发生了一系列生理生化和基因的变化,主要涉及膜流动性改变、代谢酶活性降低、活性氧(ROS)积累以及胁迫响应蛋白、脯氨酸和多胺等渗透调节物质大量积累,它们激活冷胁迫相关基因,促进细胞膜系统的重建和膜内外物质平衡,以适应低温环境^[41]。低温在植物体内的反应机制,普遍认同的理论是低温胁迫引起细胞膜黏性的增加,激活膜上的Ca²⁺通道,使Ca²⁺大量产生,激活了植物冷胁迫的响应。丙二醛含量可作为判断膜系统损伤程度和植物抗逆性的重要指标之一,具有很强的细胞毒性^[42]。陈博等^[43]发现随着植物器官中丙二醛的迅速积累,膜组织中的离子发生渗漏,膜透性发生改变,电解质外渗,相对电导率逐渐上升,进而对膜系统造成一定程度的伤害。潘翠萍等^[44]对6个不同枇杷品种在低温胁迫下的生理响应的研究表明,LT₅₀越高的枇杷丙二醛含量变化幅度越剧烈,LT₅₀越低的枇杷丙二醛含量变化幅度越平缓,这与本试验的结果相吻合。本试验研究显示,在整个低温胁迫过程中,抗寒性弱的M26和T337丙二醛含量变化幅度较大且维持较高水平,抗寒性强的SH1、Y-1和B9丙二醛含量变化幅度较小且维持较低水平,这与史清华等^[45]通过测定杨树幼苗器官中丙二醛含量得出同样的结论。

渗透调节作用是植物抵御逆境的重要生理机制,植物可通过合成渗透调节物质(脯氨酸、可溶性糖、可溶性蛋白和有机酸等)来参与调节细胞渗透平衡以增加植物自身的抗性,从而抵制生物胁迫和非生物胁迫对植物造成的伤害^[46]。植物受到逆境环境的胁迫,大多数情况下通过体内会主动积累和聚集渗透调节物质,以提高细胞液浓度^[47-48]。可溶性糖和游离脯氨酸是重要的渗透调节物质,它们的增加积累不但能提高细胞的保水能力,还能防止活性氧对膜脂和蛋白质的过氧化,对生物膜起到保护和守卫作用^[49]。可溶性糖可提高细胞液浓度,降低细胞水势,增加细胞的保水能力,从而降低冰点;还能促进ABA积累,诱导蛋白质的合成,从而提高果树的抗寒性^[50]。脯氨酸作为植物体内最有效的渗透调节物质,可保持原生质与低温胁迫下的渗透平衡,防止失水,当植物受到逆境胁迫时脯氨酸开始表现出迅速增加。本研究发现,抗寒能力强的SH1、Y-1和B9的可溶性糖含量在接近半致死温度范围时增加幅度明显高于抗寒能力较弱的M26和T337,这一研究结果与艾克来木·艾合买提等^[51]在栽培库尔勒香梨品种间抗寒能力的表现一致。本研究还发现,在-40℃时随着低温胁迫程度的增加,各砧木枝条的可溶性糖含量均呈现下降的趋势,这说明各砧木的渗透调节代谢系统遭到破坏,使其相关酶的合成受阻,该现象与吉春容等^[52]对在低温胁迫下枣树枝条的研究结果基本相符。植物响应环境胁迫积累的渗透调节物质是植物自身应对被攻击的一种防御性行为,一旦当植物超过耐受范围达到阈值时会迅速失去自我保护能力,开始受到损伤而造成不可逆转的现象。

3.3 低温胁迫与抗氧化酶活性之间的关系

植物体内活性氧清除系统包括非酶促和酶促抗氧化系统,非酶促抗氧化系统主要由抗坏血酸和还原性谷胱甘肽组成,酶促抗氧化系统主要由超氧化物歧化酶、过氧化氢酶、过氧化物酶、谷胱甘肽还原酶和脱氢抗坏血酸还原酶等组成^[49-50]。本研究发现,SOD和POD活性表现为SH1、Y-1和B9的高于T337和M26。B9的SOD、POD活性下降幅度出现在-25℃,SH1和Y-1的SOD、POD活性下降幅度出现在-30℃时,而抗寒性较弱的T337和M26在低温胁迫后SOD、POD活性变幅整体较大。杨盛等^[53]的研究表明低温处理后植物体内的酶高于正常水平。本研究发现不同苹果砧木品种的酶活性变化幅度明

显不同,抗寒性较强的品种受低温胁迫时酶活性增加幅度大,而抗寒性较弱的品种酶活性增加幅度较小,且随着低温胁迫的加剧,酶活性又迅速下降,说明轻度低温胁迫下,通过提高酶活性来减轻低温胁迫的伤害,在胁迫程度增加时活性氧积累超过保护酶系统的清除能力,进而对抗氧化酶系统造成伤害导致其活性下降。本研究发现5个苹果砧木枝条的SOD和POD酶活性随着温度的降低变化趋势相似,呈先升后降的规律,这可能是温度的急剧降低,细胞膜受害程度加重,高浓度的自由基超过伤害阈值,导致膜蛋白分子破坏,从而降低了SOD和POD活性^[52]。通过比较5个抗寒性不同苹果砧木的酶活性发现,抗寒性强的B9、SH1和Y-1的SOD和POD活性较高,抗寒性弱的T337和M26活性始终保持在较低水平,这与杨盛等^[53]和陈新华等^[54]分别在梨和甜樱桃等园艺作物上的研究结果相符。

4 结 论

通过人工模拟低温环境,测定5个苹果砧木枝条的相对电导率并结合Logistic方程计算半致死温度,以及测定低温胁迫下丙二醛、可溶性糖、游离脯氨酸含量和保护性酶类活性,结合隶属函数计算各项指标的平均隶属度评判结果与半致死温度的验证结果一致。5个苹果砧木枝条的抗寒性由强到弱依次为B9>SH1>Y-1>M26>T337。

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