

不同生态型杜梨对缺铁胁迫的生理响应及耐缺铁性评价

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摘要:【目的】杜梨在中国分布广泛,常被用作梨砧木。探索不同生态型杜梨的耐缺铁性及其机制,为解决梨树缺铁问题提供理论依据。【方法】以来源于山东、甘肃、河南3个地区的杜梨实生苗为试材,利用沙培的方法,通过比较不同生态型杜梨的缺铁胁迫生理响应差异,进行耐缺铁性评价。【结果】3种不同生态型的杜梨在正常情况下生长势不同,以山东杜梨最强,甘肃杜梨次之,河南杜梨最弱。缺铁影响杜梨生长,以生长量大的山东杜梨受到的影响最大,甘肃杜梨次之,河南杜梨最小。株高、干质量和叶片黄化指数等能一定程度反映植株缺铁状况。缺铁不同程度地降低了3种不同生态型杜梨叶片的叶绿素含量和净光合速率,甘肃杜梨的净光合能力受缺铁影响最大,山东杜梨次之,河南杜梨最小,这与其叶片黄化指数变化一致。在缺铁处理下,3种杜梨的根尖数和根表面积显著增加,河南杜梨的根尖数增加幅度和幼苗根际酸化能力显著高于其他2种生态型的杜梨,同时,根系 Fe^{3+} 还原酶活性与根际酸化能力变化提高趋势一致,各器官中的全铁和活性铁含量也以河南杜梨最高,根部活性铁和全铁积累量以山东杜梨最高,甘肃杜梨最低。3种杜梨各器官中的氮、磷、钾元素含量受缺铁影响最大的是甘肃杜梨,河南杜梨最小,山东杜梨居中。【结论】不同生态型的杜梨对缺铁胁迫生理响应敏感性不同,综合不同生态型杜梨本身生长势及对缺铁的响应,认为河南杜梨和山东杜梨的耐缺铁性优于甘肃杜梨。

关键词:杜梨;生理响应;砧木;缺铁胁迫

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Physiological response to iron deficiency stress and evaluation of tolerance to iron deficiency of different ecotypes of *Pyrus betulifolia*

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Abstract: 【Objective】 *Pyrus betulifolia* is widely distributed in China, and is often used as rootstock for pear. Previous study has showed that the tolerance to iron deficiency of different ecotypes of *P. betulifolia* are different. The aim of this study was to study the difference of physiological response to iron deficiency of different ecotypes of *P. betulifolia*, in order to provide theoretical basis for breeding iron-efficient rootstocks for pear. 【Methods】 The seedlings of *P. betulifolia* from Shandong province, Gansu province and Henan province were used as experimental materials. The seed germination was accelerated under the condition of 4 °C, and the seed sowing was carried out after blanching. The seedlings with same height and 10 true leaves were transplanted into the hole dish with high purity quartz sand as the matrix. Three iron supply concentrations, 0 $\mu\text{mol} \cdot \text{L}^{-1}$, 20 $\mu\text{mol} \cdot \text{L}^{-1}$ and 40 $\mu\text{mol} \cdot \text{L}^{-1}$ were set, and the seedlings were irrigated with the nutrient solutions every 5 days the during treatments. 【Results】 Under normal conditions, the growth vigors of different ecotypes of *P. betulifolia* were different, the strongest was *P. betulifolia* collected from Shandong (SD), followed by *P. betulifolia* collected from Gansu (GD),

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and the weakest is *P. betulifolia* collected from Henan (HD). The plant height and dry and fresh weight of Henan *P. betulifolia* were significantly higher than those of the other two ecotypes of *P. betulifolia*. The iron deficiency affected the growth of *P. betulaefolia*, SD was affected most seriously, followed by GD and HD. Plant height, dry weight and leaf yellowing index can reflect iron deficiency to a certain extent. During the test period, iron deficiency had no significant effect on stem diameter of the three different ecotypes of *P. betulifolia*. When the iron concentration was $20 \mu\text{mol} \cdot \text{L}^{-1}$, the chlorosis index of GD was significantly higher than that of HD and SD, and when the iron concentration was $0 \mu\text{mol} \cdot \text{L}^{-1}$, the chlorosis index of GD and SD was significantly higher than that of HD. The plant height of SD decreased most obviously, while that of HD decreased most lightly. The effect of iron deficiency on the aboveground part of *P. betulifolia* seedlings was greater than the underground part. The iron deficiency reduced the chlorophyll content and net photosynthetic rate of leaves of three different ecotypes of *P. betulifolia*. The net photosynthetic capacity of GD was most affected by iron deficiency, followed by SD and HD, which was consistent with the change of leaf chlorosis index. Under the iron deficiency stress, the root tip number and root surface area of the three ecotypes increased significantly. The increase range of root tip number and rhizosphere acidification ability of the seedlings of HD was significantly higher than those of the other two ecotypes. The results showed HD had the strongest root growth vigor, SD and GD had the weakest root growth vigor under the iron deficiency stress. The rhizosphere acidification capacity change trend was consistent with the increase of root Fe^{3+} reductase activity. The iron deficiency led to the unbalanced decline of iron content in the organs of the seedlings, and the decrease of active iron in the roots and new leaves was larger than that of the total iron. Among the three ecotypes, the decrease of active iron in GD was the largest, followed by SD and HD. The accumulation of the active iron and total iron in the roots was the lowest in GD. When the concentration of iron supply was $0 \mu\text{mol} \cdot \text{L}^{-1}$, the root total iron accumulation in SD was significantly higher than that in HD, but there was no significant difference in the root active iron accumulation. The effects of the iron deficiency on the contents and distribution of nitrogen, phosphorus and potassium elements in different organs of the three different ecotypes were different. The iron deficiency resulted in decreased absorption of nitrogen and phosphorus to a certain extent, but increased absorption of potassium. The contents of nitrogen, phosphorus and potassium in the organs of the three ecotypes also decreased due to the iron deficiency stress. GD was affected most obviously, HD was affected most lightly, and SD was in the middle. 【Conclusion】 The sensitivity of physiological response to the iron deficiency stress was different of three ecotypes of *P. betulaefolia*. The seedlings of *P. betulifolia* collected from Henan and Shandong had better iron deficiency tolerance than those of *P. betulifolia* collected from Gansu.

Key words: *Pyrus betulifolia*; Physiological response; Root stock; Iron deficiency stress

铁是植物生长发育必需的微量元素,参与了植物的光合作用、呼吸作用等代谢过程^[1]。缺铁直接引起植物叶片黄化,梨在生长期因缺铁引起的黄化病在中国新疆、渭北、四川盆地、黄河故道^[2-4]等梨树种植区是常见的。目前虽然通过土壤施肥、枝干注射、叶片喷施铁肥及喷施激素^[5-6]等方法提高土壤中有效铁含量和树体中铁的移动性,可以在一定程度上矫正果树缺铁失绿问题,但是不能从根本上解决植物的缺铁问题^[7]。有研究表明,砧木影响嫁接品

种对铁元素的吸收与利用^[8],选育铁高效的砧木,可以提高品种对铁的吸收利用效率^[9-10]。中国是世界梨属植物重要的起源中心^[11-12],有丰富的梨砧木资源,其中杜梨(*Pyrus betulifolia*)抗寒、抗旱、耐盐碱、适应性强^[13-16],广泛分布于中国华北、西北、东北南部等地,常被用作梨的砧木。前期的研究发现,不同生态型的杜梨对铁的吸收能力不同。因此,笔者在本试验中通过研究杜梨缺铁生理响应的差异性,对不同生态型的杜梨进行耐缺铁性评价,筛选对缺铁耐

性强的杜梨类型,为选育铁高效砧木、解决梨树缺铁问题提供理论依据。

1 材料和方法

1.1 试验材料及处理

参试杜梨种子分别采自山东省临沂市临沭县、甘肃省庆阳市宁县和河南省洛阳市栾川县三处具有代表性的野生杜梨群体,每处种源地采种的杜梨群体均大于 30 株,混合采种后用于以下试验。为了表述方便,依据产地分别用 SD(山东杜梨)、GD(甘肃杜梨)和 HD(河南杜梨)表示。选择大小一致饱满的种子,经灭菌处理后置于垫有湿纱布的培养皿中,置于 4 °C 的条件下催芽。种子露白后进行穴盘播种,穴盘营养土体积比为草炭:珍珠岩=4:1。

选取高度一致、10 枚真叶的幼苗移栽到高纯度石英砂作基质的穴盘中,穴盘尺寸为 56 cm×32 cm×16 cm(28 孔)。石英砂粒径组成:>2 mm 的占 1%,>1~2 mm 占 9%,>0.5~1.0 mm 占 20%,<0.5 mm 占 70%^[17]。完全营养液缓苗 2 周后用于试验处理。完全营养液参照 Ma 等^[18]的方法配置。试验设 0、20、40 $\mu\text{mol}\cdot\text{L}^{-1}$ FeNa-EDTA 3 个供铁浓度处理,每个处理有不同生态型杜梨幼苗各 84 株,每个重复 28 株,共 3 个重复,处理期间每隔 5 d 浇灌 1 次营养液,每次每穴浇灌 50 mL。初始营养液的 pH 用 NaOH 或 HCl 调至(6.0±0.1)。处理 60 d 后进行指标测定。试验在人工气候室进行,温度为 22~27 °C,相对湿度为 65%~85%,光照度为 8000~10 000 lx,光照时间为 14 h。

1.2 叶片黄化指数分级及其统计

根据叶片黄化程度,将叶片的黄化级值分为 5 个等级^[19]:

0 级,完全没有发生黄化。

1 级,叶片边缘轻微黄化,黄化不超过 1/2。

2 级,叶片脉间黄化加重,黄化不超过 3/4。

3 级,叶片脉间失绿,全叶黄化。

4 级,叶片严重失绿甚至白化,叶边缘焦枯,严重的全叶焦枯(图 1)。

取每株新叶(茎端的 3 枚完全展开叶片),确定其黄化级数,按以下公式计算每个单株黄化指数:黄化指数/%=[\sum (黄化级值×相应黄化级值叶片数)/(总叶片数×4)]×100。取平均值作为该生态型杜梨的黄化指数,反映其黄化程度。

1.3 叶绿素含量的测定



图 1 叶片黄化指数分级

Fig. 1 Index grading of leaf yellowing

采用手持 SPAD-502 叶绿素仪(Konica Minolta, 日本)对梨幼苗相同部位的新叶进行测定。

1.4 生长指标的测定

植物干质量的测定:鲜样称质量后在烘箱中 105 °C 杀青 20~30 min,然后在 85 °C 恒温烘干至恒质量,用电子天平(万分之一)称量质量(g)。根冠比值=根干质量/(茎干质量+叶干质量)。

1.5 根际酸化能力的测定

参照殷文娟等^[20]的方法并加以改进,将营养液初始 pH 调为 6.00,把不同处理的梨幼苗放进 50 mL 营养液中,24 h 后测定根际溶液 pH,以营养液 pH 变化来衡量根系酸化能力。

1.6 净光合速率的测定

使用 CIRAS-3 便携式光合仪(PP Systems, 美国)进行测定。在晴朗上午 10:00—11:00 测量植株新叶的净光合速率(P_n),使用荧光叶室,光质为红蓝光,光照度设定为 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$,CO₂浓度 380~450 $\mu\text{L}\cdot\text{L}^{-1}$,叶片温度(25±1)°C,气体流速 300 mL·min⁻¹,空气湿度 65%~85%^[21]。

1.7 根系 Fe³⁺还原酶活性的测定

参照许良政等^[22]的方法进行测定,设 Fe(II)-联吡啶的摩尔吸收系数为 8 650 mol·L⁻¹·cm⁻¹,反应时间(t)为 2 h,比色波长为 523.3 nm。按下列公式计算还原酶活性:还原酶活性($\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$)=(8650×10⁶)/(FW×OD)。

1.8 根系表面积和根尖数的测定

将整株幼苗根系洗净后,使用根系扫描仪(Epson Perfection V800 photo)扫描之后,用根系分析软件(WinRHIZO 2007 版)对根体积及总根尖数进行测定分析。

1.9 全铁和活性铁含量及根系全铁和活性铁积累量的测定

全铁和活性铁含量均使用 ICP-OES (Opti-

ma8000,美国)进行测定。全铁含量测定前处理:称取1.00 g干样置三角瓶中,加优级纯硝酸10 mL和高氯酸2 mL,于180 °C消解至1 mL左右停止加热。加入10 mL超纯水,沸腾3~5 min,超纯水定容50 mL后上机测定。活性铁含量测定前处理:参考黄宏文^[23]的方法,略有改动:将鲜样烘干磨成粉末,称取1.00 g,放入具塞试管,加入10 mL的0.1 mol·L⁻¹稀盐酸连续振荡12 h浸提后过滤,上机测定。根系全铁或活性铁积累量(mg·plant⁻¹)=根系干质量×根系全铁或活性铁含量。

1.10 氮元素和其他矿质元素含量测定

样品于105 °C杀青30 min,80 °C烘干至恒质量,粉碎过0.25 mm筛后,采用凯氏定氮法^[24]进行测定。其他矿质元素含量测定方法同全铁含量测定。

1.11 数据处理

用Microsoft Excel处理数据,Graph pad prism6软件作图,DPS软件在 $p < 0.05$ 的水平上计算最小显著性差异(LSD)值。

2 结果与分析

2.1 缺铁对不同生态型杜梨幼苗生长的影响

缺铁明显影响了杜梨幼苗的生长,受影响的程度随着缺铁程度的增加而增加,但不同生态型的杜梨幼苗生长受影响的程度不同。山东杜梨(SD)本身生长势比其他两个生态型的杜梨强,缺铁对其株高的影响最大。由表1可以看出,SD株高40 $\mu\text{mol}\cdot\text{L}^{-1}$ 处理显著大于20 $\mu\text{mol}\cdot\text{L}^{-1}$ 处理,显著大于0 $\mu\text{mol}\cdot\text{L}^{-1}$ 处理;而甘肃杜梨(GD)株高40 $\mu\text{mol}\cdot\text{L}^{-1}$ 处理显著高于0 $\mu\text{mol}\cdot\text{L}^{-1}$ 处理,但二者与20 $\mu\text{mol}\cdot\text{L}^{-1}$ 处理无显著差异;河南杜梨(HD)株高是3种杜梨中最矮的,虽然也受到缺铁的影响,但影响最小,处理间差异不显著。植株干质量(根和冠)测定结果与株高相似,也随着缺铁程度的增加而显著下降。正常干质量较大的SD受到缺铁影响的程度显著高于GD和HD。由根冠比可以看出,除HD在供铁浓度为20 $\mu\text{mol}\cdot\text{L}^{-1}$ 时差异不显著外,均表现了对地上部的

表1 不同铁浓度处理对不同生态型杜梨幼苗生长指标的影响

Table 1 Effects of different iron concentrations on growth indexes of different ecotypes of *P. betulifolia*

品种 Variety	c(铁) Iron concentration/ ($\mu\text{mol}\cdot\text{L}^{-1}$)	株高 Height of plant/cm	茎粗 Diameter of stem/mm	根干质量 Root dry mass/g	冠干质量 Shoot dry mass/g	根冠比 Root shoot ratio
SD	0	18.9±2.4 c	2.61±0.32 abc	0.87±0.10 e	1.20±0.09 e	0.73±0.03 f
	20	21.3±3.2 b	2.64±0.31 ab	1.26±0.12 b	1.86±0.12 b	0.68±0.03 g
	40	23.3±3.4 a	2.65±0.33 a	1.53±0.13 a	2.43±0.13 a	0.63±0.02 h
GD	0	13.1±1.9 efg	2.41±0.19 c	0.72±0.09 f	0.81±0.10 f	0.88±0.03 b
	20	14.9±1.6 de	2.44±0.17 abc	1.06±0.15 d	1.30±0.15 d	0.82±0.03 d
	40	15.3±1.5 d	2.50±0.20 abc	1.16±0.15 c	1.49±0.14 c	0.78±0.03 e
HD	0	12.2±2.6 g	2.43±0.21 bc	0.69±0.11 f	0.75±0.11 f	0.91±0.06 a
	20	13.8±1.8 defg	2.58±0.32 abc	1.01±0.12 d	1.18±0.12 e	0.86±0.02 c
	40	13.9±1.9 defg	2.57±0.33 abc	1.19±0.10 bc	1.40±0.10 c	0.85±0.02 c

注:同列不同小写字母表示不同处理间差异显著($p < 0.05$, LSD)。下同。

Note: Different lowercase letters in the same column indicate significant differences between the treatments ($p < 0.05$, LSD). The same below.

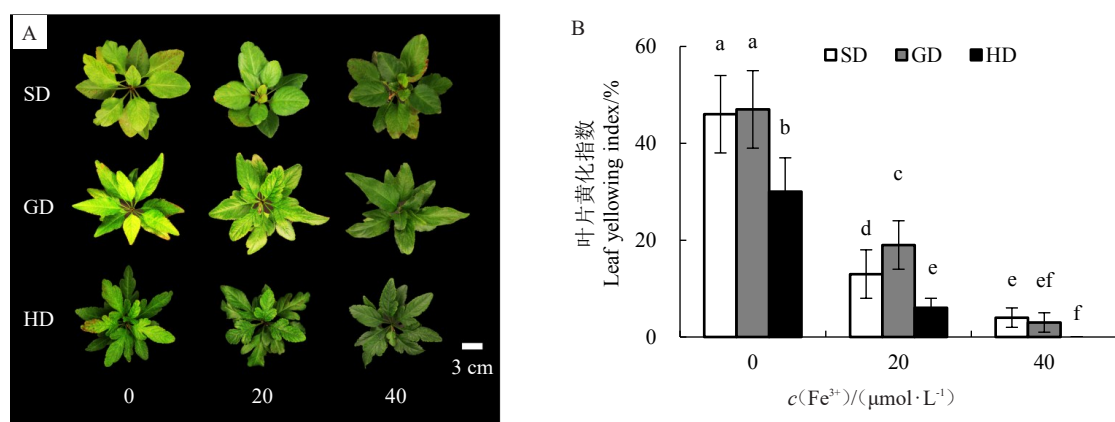
影响大于地下部。同一生态型杜梨幼苗的茎粗在不同处理间差异不显著。说明生长期内的株高、干质量可能是表征杜梨植株缺铁生长状态的良好指标。从缺铁影响生长情况看,不同生态型的杜梨生长势不同,生长量大的受影响大。因此,3种不同生态型的杜梨SD受到的影响最大,HD最小,GD居中。

2.2 缺铁对不同生态型杜梨幼苗叶片黄化及光合性能的影响

叶片黄化程度随着供铁浓度的降低而增加(图

2-A)。由图2-B可以看出,供铁浓度为40 $\mu\text{mol}\cdot\text{L}^{-1}$ 时,不同生态型杜梨的叶色有一定的差异,SD显著高于HD,说明生长量大的SD可能需要更多的铁来满足正常生长需要;当供铁浓度降低时,GD的叶片黄化指数显著高于(20 $\mu\text{mol}\cdot\text{L}^{-1}$ 处理)或类似于(0 $\mu\text{mol}\cdot\text{L}^{-1}$ 处理)SD,二者显著高于HD。综合生长量因素分析,GD更易表现缺铁黄化。

由图3-A可以看出,随着供铁浓度的降低,3种杜梨幼苗的新叶相对叶绿素含量(SPAD值)与叶片黄化指数变化相似,均呈现下降趋势。在2个缺铁



A. 叶片表型; B. 叶片黄化指数。不同小写字母表示差异显著($p < 0.05$, LSD)。下同。

A. Leaf phenotype; B. Leaf yellowing index. Different small letters indicate significant difference ($p < 0.05$, LSD). The same below.

图2 缺铁对不同生态型的杜梨幼苗叶片黄化的影响

Fig. 2 Effects of iron deficiency on leaf chlorosis of different ecotypes of *P. betulifolia* seedlings

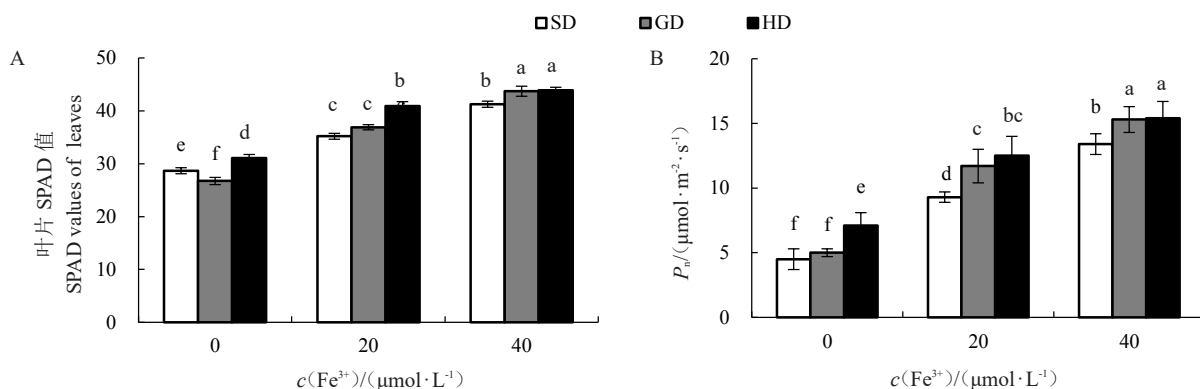


图3 缺铁对不同生态型杜梨幼苗相对叶绿素含量以及净光合速率的影响

Fig. 3 Effects of iron deficiency on relative chlorophyll content and net photosynthetic rate of different ecotypes of *P. betulifolia* seedlings

处理中,HD的SPAD值均显著高于其他2种杜梨。随着供铁浓度降低,SPAD值以GD下降幅度最大(38.8%),SD次之(30.5%),HD最小(29.2%)。由图3-B可以看出,缺铁导致净光合速率急剧下降,各处理中SD均显著低于HD。但GD的下降幅度最大,SD次之,HD最小。净光合速率的变化表现了与SPAD值变化的一致性。仅从叶片相对叶绿素含量和净光合速率对缺铁胁迫的响应看,GD对缺铁最为敏感,SD次之,而HD敏感性较低。

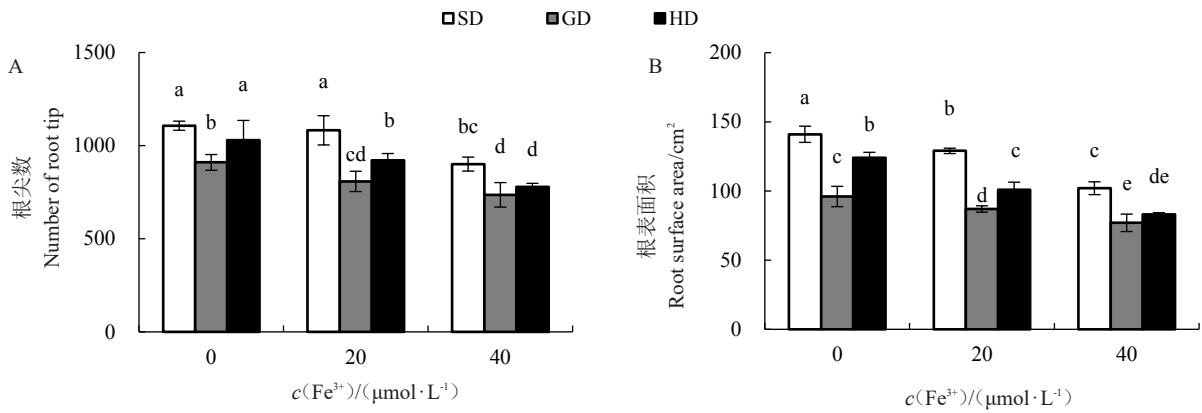
2.3 缺铁对不同生态型杜梨幼苗根系生长的影响

根尖是植物吸收矿质营养最活跃的部位,根尖数和根表面积的大小体现了根的吸收能力的强弱。由图4-A可以看出,随着供铁浓度降低,根尖数显著增加。在供铁浓度为 $40 \mu\text{mol}\cdot\text{L}^{-1}$ 时,SD根尖数显著

大于GD和HD,且GD和HD没有显著差异。当供铁浓度降为 $20 \mu\text{mol}\cdot\text{L}^{-1}$ 时,SD和HD的根尖数均显著增加,GD无显著性变化。当供铁浓度降到 $0 \mu\text{mol}\cdot\text{L}^{-1}$ 时,GD和HD显著增加,但此时SD和HD的根尖数显著大于GD,SD和HD之间无显著差异。与 $40 \mu\text{mol}\cdot\text{L}^{-1}$ 相比,HD的根尖数增加32.4%,GD增加23.5%,SD增加29.1%,由图4-B可以看出,缺铁处理也使3种杜梨根表面积显著增加,供铁浓度 $0 \mu\text{mol}\cdot\text{L}^{-1}$ 与 $40 \mu\text{mol}\cdot\text{L}^{-1}$ 相比,HD的根表面积增加49.6%,GD增加24.1%,SD增加37.7%,表明HD在缺铁胁迫下根系生长能力最强,SD次之,GD最弱。

2.4 缺铁对不同生态型杜梨幼苗根际酸化能力和 Fe^{3+} 还原酶活性的影响

植物根系在吸收铁时,首先会酸化根际环境,将



A. 每株幼苗的根尖数; B. 每株幼苗的根表面积。

A. The number of root tips per seedling; B. Root surface area of per seedling.

图4 缺铁对不同生态型杜梨幼苗根系生长的影响

Fig. 4 Effects of iron deficiency on root growth of different ecotypes of *P. betulifolia* seedlings

土壤中 Fe^{3+} 变为可溶性 Fe^{2+} ,同时通过 Fe^{3+} 还原酶将 Fe^{3+} 还原为 Fe^{2+} 进行吸收。因此植物根际酸化能力越强和 Fe^{3+} 还原酶活性越高,越有利于对 Fe^{3+} 的吸收。由图5-A可见,随着供铁浓度的降低,3种杜梨幼苗的根际pH值逐渐降低,酸化能力逐渐增强。在供铁浓度为 $40\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,3种杜梨的根际pH值没有显著差异。随着供铁浓度的降低,3种杜梨的根际酸化能力均显著增加,其中,在供铁浓度为 $0\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,GD的根际pH值显著高于HD,与SD差异不明显。说明GD的根际酸化能力最弱,可能是其更不耐受缺铁的原因之一。为了解根系酸化能力与 Fe^{3+} 还原酶活性的关系,进一步分析了不同处理 Fe^{3+} 还原酶活性变化,结果如图5-B所示。当供铁浓度为 $40\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,3种杜梨之间无显著差异,随着铁浓度的降低,3种杜梨幼苗的 Fe^{3+} 还原酶活性均显著提

高。当供铁浓度为 $20\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,HD的 Fe^{3+} 还原酶活性显著大于SD和GD,后二者之间无显著差异。当供铁浓度为 $0\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,HD的 Fe^{3+} 还原酶活性显著大于GD,但与SD差异不显著。与供铁浓度为 $40\ \mu\text{mol}\cdot\text{L}^{-1}$ 时相比,根系 Fe^{3+} 还原酶活性提高程度为 $\text{HD}>\text{SD}>\text{GD}$,与根际酸化能力表现了一致的变化。

2.5 缺铁对不同生态型杜梨幼苗各器官活性铁和全铁含量及分布的影响

铁在杜梨幼苗的根中含量最高,其次是老叶,茎和新叶相近。缺铁导致杜梨幼苗各器官的铁含量不均衡下降,尤以根、茎和新叶下降明显。如图6所示,在供铁浓度为 $40\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,根中的全铁含量HD显著高于SD和GD,后二者之间无显著差异。随着供铁浓度的降低,3种杜梨根中的全铁含量均

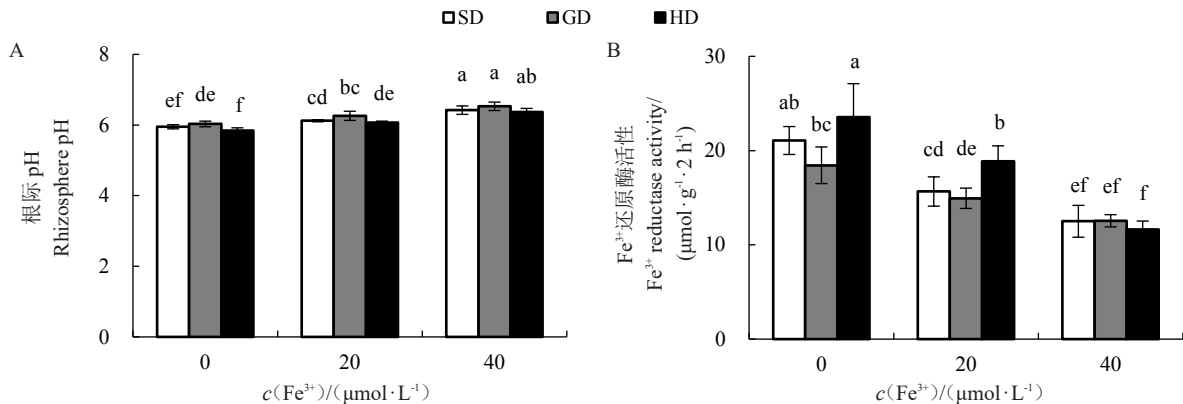
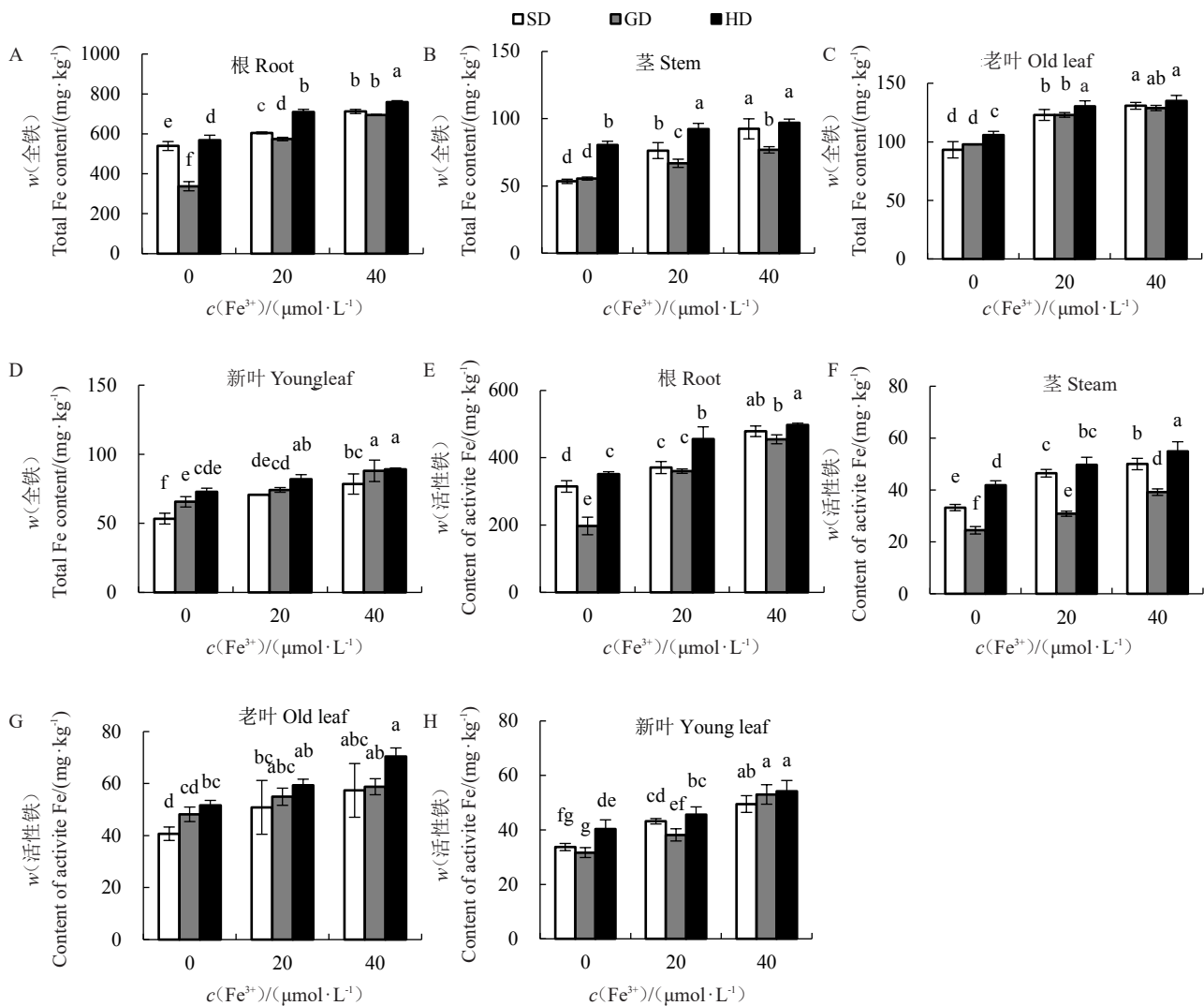


图5 缺铁对不同生态型杜梨幼苗根际酸化能力和 Fe^{3+} 还原酶活性的影响

Fig. 5 Effects of iron deficiency on rhizosphere acidification and Fe^{3+} reductase activity of different ecotypes of *P. betulifolia* seedlings



A~D. 不同器官的全铁含量;E~H. 不同器官的活性铁含量。

A-D. Total iron content in different organs; E-H. Active iron content in different organs.

图6 缺铁对不同生态型杜梨幼苗各器官全铁和活性铁含量及分布的影响

Fig. 6 Effects of iron deficiency on contents and distribution of total iron and active iron in organs of different ecotypes of *P. betulifolia* seedlings

显著下降,以GD下降幅度最大。根中活性铁含量表现了类似的变化趋势。GD茎中的全铁和活性铁的含量显著低于其他2种杜梨,HD高于SD。老叶中的全铁含量在供铁浓度为 $40\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,3种杜梨无显著差异,当供铁浓度降低到 $20\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,HD和GD无显著变化,SD老叶中的全铁含量显著降低, $0\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,3种杜梨均进一步显著降低,HD含量高于SD和GD,后二者无显著差异。活性铁含量仅在 $0\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,HD显著高于SD,但二者与GD差异不显著,其他两个处理3种杜梨间差异不显著。新叶在铁浓度为 $40\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,SD全铁含量显著低于HD和GD,当供铁浓度降低到 $20\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,HD下降不明显,SD和GD均显著下降,当供铁

浓度降低到 $0\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,3种杜梨都较前一个处理表现了显著下降。但活性铁在2个缺铁处理中,3种杜梨都随供铁浓度下降而显著下降,GD下降幅度最大。说明3种生态型杜梨根对铁的吸收、贮备和输出能力不同,缺铁导致的新叶中活性铁含量变化与根中相似。

总体上,缺铁引起根和新叶中活性铁的下降低于全铁,3种杜梨中,以GD下降幅度最大,其次SD,HD最小。

由于杜梨用作砧木时根系可作为一个功能的整体,为此,以单株根系为单位计算了缺铁对不同生态型杜梨幼苗根系全铁和活性铁积累量的影响。如图7所示,在不同供铁浓度下,SD和HD的单株根系全

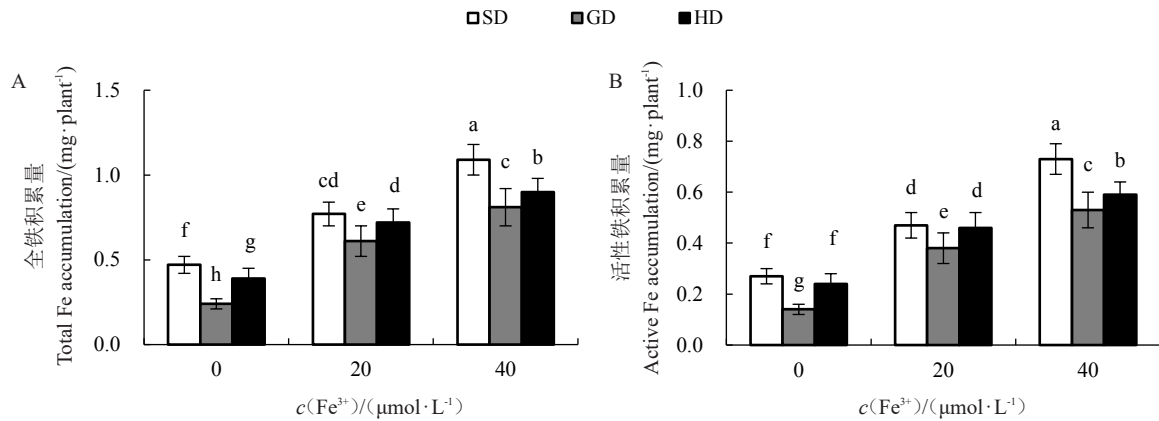


图7 缺铁对不同生态型杜梨幼苗根系全铁和活性铁积累量的影响

Fig. 7 Effects of iron deficiency on total iron and active iron accumulation in roots of different ecotypes of *P. betulifolia* seedlings

铁与活性铁积累量均显著大于GD,在供铁浓度为 $0\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,SD的根系全铁积累量显著大于HD,而SD的根系活性铁积累量与HD无显著差异。

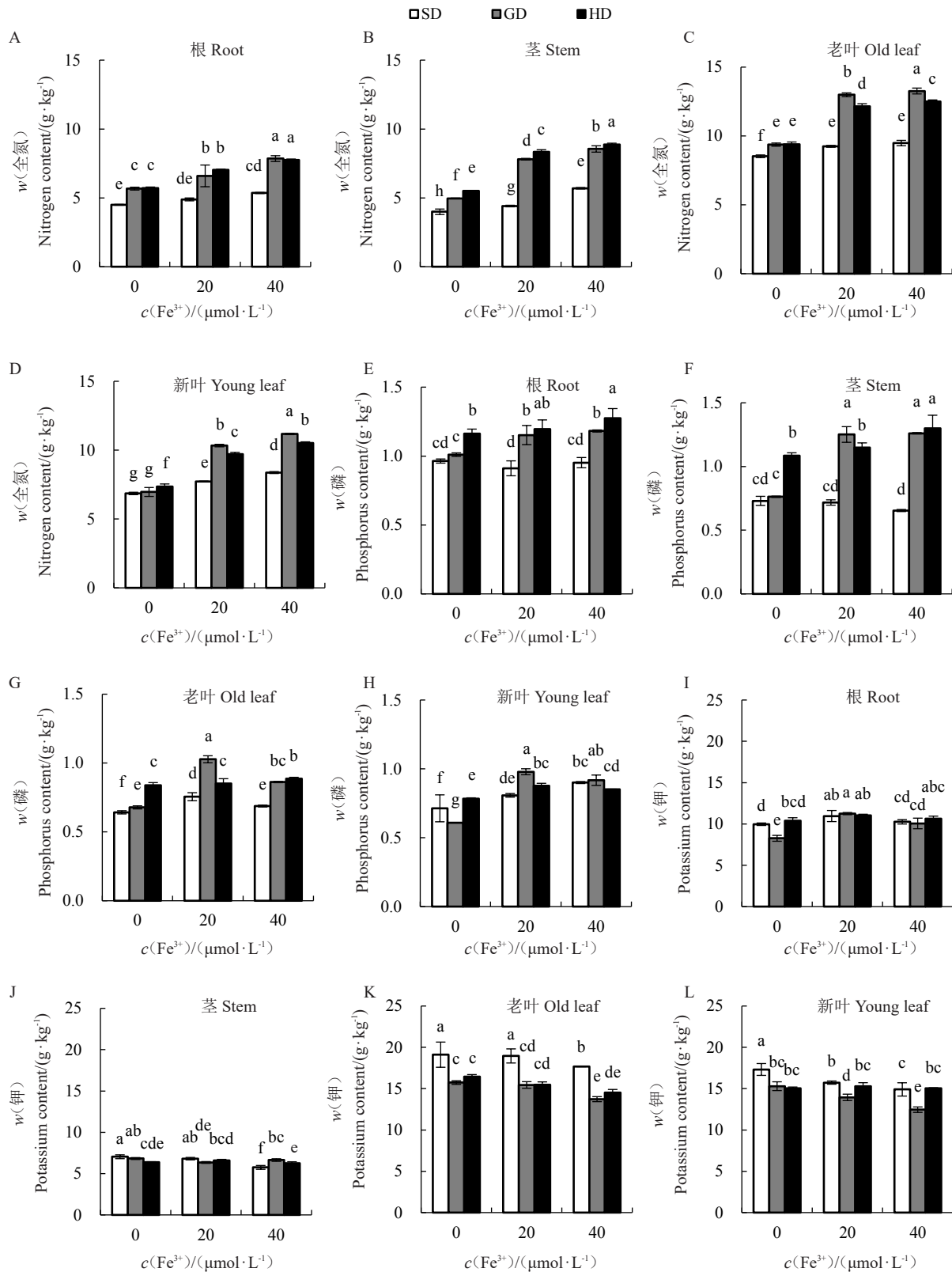
2.6 缺铁对不同生态型杜梨幼苗各器官氮、磷、钾元素含量和分布的影响

缺铁引起杜梨幼苗各器官氮含量下降(图8-A~D)。根、老叶和新叶中氮元素含量受缺铁影响程度依次为:GD>HD>SD,茎中氮元素含量受缺铁的影响程度依次为:GD>SD>HD,由此可以看出GD氮元素含量受缺铁的影响最大。由图8-E~H可以看出,缺铁对根中磷元素含量变化影响较小,除GD在供铁浓度为 $0\ \mu\text{mol}\cdot\text{L}^{-1}$ 时P元素含量呈现显著下降外,SD和HD无显著变化。3种杜梨茎中磷元素含量受缺铁影响程度依次为:GD>HD>SD,老叶依次为:GD>SD>HD。新叶中SD在供铁浓度为 $20\ \mu\text{mol}\cdot\text{L}^{-1}$ 时磷元素含量显著下降,而GD和HD无显著变化。由图8-I~L可以看出,钾元素含量受缺铁影响程度根中以GD最大,SD次之,HD变化不显著。但随着供铁浓度降低,茎、老叶和新叶中钾元素含量表现了不同程度的增加,老叶中的增加幅度为SD>GD>HD,新叶中为GD>SD,HD无显著变化。在供铁浓度由 $40\ \mu\text{mol}\cdot\text{L}^{-1}$ 降低为 $20\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,HD老叶中钾元素含量无显著变化,受缺铁影响程度最小,供铁浓度由 $20\ \mu\text{mol}\cdot\text{L}^{-1}$ 降低为 $0\ \mu\text{mol}\cdot\text{L}^{-1}$ 时,3种杜梨老叶中钾元素含量均无显著变化。总体来看,缺铁对不同生态型的杜梨各器官中氮磷钾元素含量和分布影响是不同的,其中,缺铁对GD的影响最大,SD次之,HD最小。

3 讨论

铁元素作为光合磷酸化和氧化磷酸化中铁硫蛋白的重要组成元素,参与了植物的光合和呼吸作用等代谢过程,对植物的生长发育起着重要的作用^[25-26]。结果表明,缺铁会导致杜梨幼苗的株高、茎粗和干质量下降,其中地上部干质量下降幅度大于根部,说明缺铁对地上部生长的影响大于地下部,本身生长量越大,受影响的程度越大,并与缺铁引起的叶绿素含量和净光合速率下降表现相一致。有研究结果表明地下部与地上部生长状态可能与生长素和细胞分裂素的合成与分布有关^[27-28],但这与缺铁之间的联系还不明确。根尖是根系吸收养分最活跃的部位,植物在缺铁条件下通过增加根尖数和根表面积来提高获取铁元素的效率^[29]。本研究表明随着供铁浓度降低,3种不同生态型的杜梨根尖数和根表面积均显著增大,其中HD根系生长能力最强,GD最弱,表现与各处理叶片黄化程度相一致。3种不同生态型杜梨之间的生长量不同,HD与GD的生长量相近,SD的生长量最大,根中全铁和活性铁积累量最高,因此SD表现不耐缺铁的部分原因可能与其生长量大、需要更多的铁元素有关。当SD用作为砧木时,对接穗的铁营养供应能力可能并不一定低于HD,所以还需进一步通过砧木嫁接试验来评价其在新的嫁接复合体中对铁元素的吸收和向上供应的能力。

一般情况下,土壤中铁元素主要以生物有效性低的 Fe^{3+} 形式存在,尤其是在较高的pH和碳酸盐含



A~D. 全氮含量; E~H 磷含量; I~L. 钾含量。

A-D. Total nitrogen content; E-H. Phosphorus content; I-L. Potassium content.

图 8 缺铁对不同生态型杜梨幼苗各器官氮、磷、钾元素含量及分布的影响

Fig. 8 Effects of iron deficiency on contents and distribution of nitrogen, phosphorus and potassium in organs of different ecotypes of *P. betulifolia* seedlings

量的土壤中,铁的溶解度严重降低^[30],杜梨作为双子叶植物,主要运用策略 I^[31]来进行铁元素的转运吸收。因此在吸收环境中的铁元素时,首先通过根尖分泌质子和有机酸,利用 Fe^{3+} 还原酶将 Fe^{3+} 还原成 Fe^{2+} ,然后转运到地上部^[32-33]。当出现缺铁逆境时,根际酸化能力和 Fe^{3+} 还原酶活性等生理响应程度可作为衡量植物耐缺铁能力的重要依据^[34],在根际酸化能力和 Fe^{3+} 还原酶活性,HD表现最强,这也可能是相同条件下黄化程度轻的原因之一。活性铁和全铁含量可以直接反映树体对缺铁响应能力的大小^[35-36],缺铁会引起根、茎、叶各器官中的活性铁和全铁含量不均衡的降低,笔者在本研究中发现HD根和茎的全铁含量和活性铁含量均要显著高于SD和GD,表明HD对铁的吸收和运输能力均强于SD和GD。综合考虑,3种不同生态型的杜梨对铁缺乏的生理响应能力为 $\text{HD} > \text{SD} > \text{GD}$ 。

植株缺铁时,还会影响氮、磷、钾和其他矿质元素的吸收^[37-39],氮素是果树必需的大量营养元素之一,果树缺氮会造成叶片失绿,净光合能力下降,影响果实质量和产量^[40],本研究结果表明杜梨幼苗各器官的氮、铁元素含量具有协同作用,氮元素含量会随着活性铁和全铁含量的下降而下降,其中SD根部的氮吸收和叶的氮代谢利用能力及HD茎的氮运输能力受缺铁影响较小。磷与碳水化合物和脂肪蛋白质的合成、转运有关,缺磷影响地上部的生长,导致叶片疏小,叶色褐黄至紫色^[41]。笔者在本研究中发现缺铁会降低植株对磷元素的吸收,进而加重缺铁对植株的不利影响,磷元素含量受缺铁影响最大的是SD,GD次之,HD最小。钾元素参与了植物体内多种酶的活化及渗透调节^[42-43],缺铁会引起杜梨茎和叶中钾元素含量出现不同程度的增加,这种现象在番茄中也有类似的报道^[44],但不同生态型的杜梨各组织器官受影响的程度不同,因此,铁和其他矿质营养元素之间协同作用的差异可能也是其耐缺铁性不同的原因之一。

4 结 论

不同生态型杜梨缺铁胁迫生理响应及耐缺铁性存在较大差异,缺铁条件下甘肃杜梨的叶片黄化程度最高,山东杜梨次之,河南杜梨最低,缺铁使叶片净光合能力下降程度最大的是甘肃杜梨,河南杜梨的根际酸化能力和 Fe^{3+} 还原酶活性最高,根系生长

能力最强,活性铁和全铁含量最高,对氮、磷、钾元素的吸收影响最小,根部活性铁和全铁积累量以山东杜梨最高,不同生态型杜梨对缺铁胁迫生理响应敏感性不同,综合不同生态型杜梨本身生长势及对缺铁的反应,认为河南杜梨和山东杜梨的耐缺铁性优于甘肃杜梨。

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