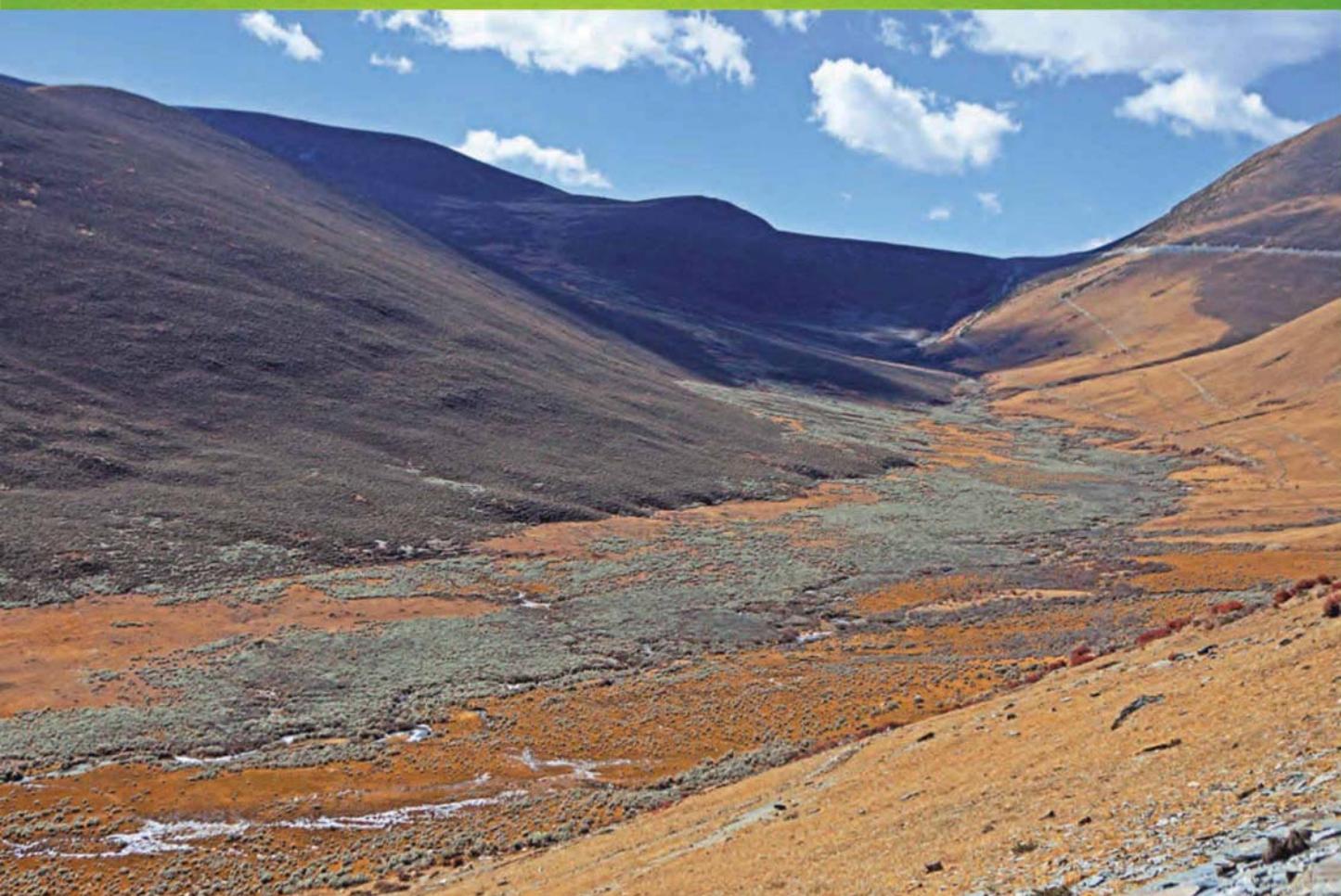


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封面图说: 川西高山地带土壤及植被——青藏高原东缘川西的高山地带坡面上为草地, 沟谷地带由于低平且水分较充足, 生长有很多灌丛。川西地区大约在海拔 4000m 左右为林线, 以下则分布有亚高山森林。亚高山森林是以冷、云杉属为建群种或优势种的暗针叶林为主体的森林植被。作为高海拔低温生态系统, 高山-亚高山地带土壤碳被认为是我国重要的土壤碳库。有研究表明, 易氧化有机碳含量与海拔高度呈显著正相关, 显示高海拔有利于土壤碳的固存。因而, 这里的表层土壤总有机碳含量随着海拔的升高而增加。

彩图及图说提供: 陈建伟教授 北京林业大学 E-mail: cites.chenjw@163.com

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王宇涛, 李春妹, 李韶山. 华南地区3种具有不同入侵性的近缘植物对低温胁迫的敏感性. 生态学报, 2013, 33(18): 5509-5515.

Wang Y T, Li C M, Li S S. Chilling sensitivities of three closely related plants with different invasiveness in South China. Acta Ecologica Sinica, 2013, 33(18): 5509-5515.

华南地区3种具有不同入侵性的近缘植物 对低温胁迫的敏感性

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摘要: 以五爪金龙(*Ipomoea cairica* (L.) Sweet, 重度入侵植物)、裂叶牵牛(*Ipomoea nil* (L.) Choisy, 轻度/非入侵植物)和三裂叶薯(*Ipomoea triloba* L., 非入侵植物)3种起源于热带美洲、且在华南地区具有不同入侵性的番薯属藤本植物作为研究对象, 通过比较它们在低温胁迫下的生理响应探究3种植物对低温的敏感性与它们入侵性之间的关系。通过测定在不同温度(28、15、10 °C)处理下植物的生物量、活性氧、渗透调节物质、根系活力、光合特征等生理指标发现, 五爪金龙、裂叶牵牛及三裂叶薯均通过增加光合系统II的热耗散、积累渗透调节物质以及增强根系活力来应对低温环境, 但15 °C的温度条件已经对3种植物形成较为强烈的胁迫作用, 表现为H₂O₂和丙二醛的积累、光合系统II受损、根部细胞死亡以及生物量、根长的极显著下降($P<0.01$), 证明3种植物对低温胁迫均具有较高的敏感性。综合比较3种植物各生理指标的响应幅度发现, 它们对低温的耐受性表现为: 五爪金龙 > 裂叶牵牛 > 三裂叶薯, 这与它们在华南地区的入侵危害程度一致, 暗示低温敏感性的差异可能是其入侵性差异的重要原因。结果表明, 低温敏感性是影响外来植物入侵性和入侵区域的重要因素, 五爪金龙较高的低温敏感性是限制其在华南以外地区形成入侵危害的重要原因。

关键词: 外来入侵植物; 入侵性; 五爪金龙; 裂叶牵牛; 三裂叶薯; 低温敏感性

Chilling sensitivities of three closely related plants with different invasiveness in South China

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Abstract: Chilling is an important constraint factor to the growing development and geographic distribution of plant species. *Ipomoea cairica* (L.) Sweet is one of the most notorious invasive weeds in South China, while it seems to be not invasive outside South China. *Ipomoea nil* (L.) Choisy (slightly invasive or non-invasive) and *Ipomoea triloba* L. (non-invasive) are two of the *I. cairica*'s closely related species that are also originated from the tropical America. In the present study, we compared the chilling sensitivities of these three vine plants by testing their ecophysiological responses to low-temperature treatments (15 °C, 10 °C) in a hydroponic experiment, so as to illustrate the potential connections between the chilling sensitivity and invasiveness. We hypothesized that (i) the three alien plants were all sensitive to chilling stress and (ii) the chilling sensitivity of the non-invasive (or slightly invasive) plants *I. triloba* and *I. nil* were higher than that of the serious invasive species *I. cairica*.

Cuttings of *I. cairica*, *I. nil* and *I. triloba* collected from selected habitats in South China were planted in water to let the root grow for one week, and then cultivated in Hoagland nutrient solution for 4 weeks. Similarly sized plants of each species were placed in the light incubators with different temperatures (28 °C, 15 °C, 10 °C) for 8 days. The chlorophyll

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fluorescence technique was used to monitor the photosynthetic apparatus of these *Ipomoea* plants every other day. After harvest the shoot biomass and root length of new growth for all plants were calculated. The accumulation of H₂O₂, malodialdehyde (MDA), proline and soluble carbohydrate in the leaves, as well as the root metabolic activity and membrane integrity were also tested as indications of physiological performance after different temperature treatments.

The chlorophyll fluorescence results showed that photosystem II (PS II) of all three *Ipomoea* species was partly damaged by chilling (15 °C, resulted in increased initial fluorescence level (F_0), but decreased electron transport rate (ETR) and maximum photochemical efficiency (F_v/F_m)), especially for *I. triloba*, which always was most sensitive. There was also higher non-photochemical quenching (NPQ) under chilling stress in all three species, indicating increased thermal dissipation in PS II. Compared to the control (28 °C), all plants under chilling stress accumulated significantly more proline and soluble carbohydrate ($P<0.01$), both of which could improve their chilling tolerance. There were significantly less shoot biomass and root length of new growth, and higher levels of cell membrane integrity in roots under the 15 °C and 10 °C treatment for all three species ($P<0.05$), and that should be partly attributed to the accumulation of H₂O₂ and MDA, which were observed in all of the plants under chilling stress. These results clearly showed that at 15 °C there had been significant stress effects in these *Ipomoea* species. The first hypothesis of this research, i.e. the three species have high chilling sensitivities, was thus supported. As for the other aspect, when comparing the response intensities of the three *Ipomoea* species to chilling treatment, it is found that at the 10 °C treatment only *I. cairica* has continued to grow, while no growth was observed in *I. nil* and *I. triloba* during the periods of chilling stress, indicating that *I. cairica* has the highest chilling tolerances among the three species. The second hypothesis of this study was thus also supported. Besides, among the three *Ipomoea* species, *I. triloba* seems to be the most sensitive one to chilling as it usually had the highest physiological response intensities to chilling stress. The results from this study implied that the comparatively higher chilling tolerance of *I. cairica* in comparison to *I. nil* and *I. triloba* should be one of the reasons that in South China it is more invasive than the latter two species. The chilling sensitivity is an important key factor to the invasiveness of alien plants. Besides, the relatively high chilling sensitivity of *I. cairica* should be one of the most important reasons that it has not invaded other areas than South China. Therefore, it is necessary to pay more attention to the potential range expansion of *I. cairica* under the background of global warming.

Key Words: alien invasive plant; invasiveness; *Ipomoea cairica*; *Ipomoea nil*; *Ipomoea triloba*; chilling sensitivity

温度是自然界中限制植物生长发育以及地理分布最重要的生态因素之一^[1]。热带或亚热带地区全年气候较为温暖,因此分布于该区域的植物种类大多缺乏对低温环境的耐受性^[2]。五爪金龙(*Ipomoea cairica* (L.) Sweet,旋花科番薯属)是一种原产于热带美洲的多年生藤本植物,近年来在我国华南地区形成严重的入侵态势。野外观察发现,它们通过快速的攀援生长在较短的时间内形成覆盖其它植物的优势种群,实现成功入侵^[3]。它们的化感效应^[4]以及耐盐、耐草食动物(昆虫)啃食的特征^[5]在其入侵过程中也发挥了重要作用。尽管五爪金龙已成为目前华南地区最具危害的恶性杂草之一^[6],它们在华南以外的区域却并未形成入侵危害。

同样原产于热带美洲的旋花科番薯属植物三裂叶薯(*Ipomoea triloba* L.)和裂叶牵牛(*Ipomoea nil* (L.) Choisy)是华南地区常见的1年生藤本植物。三裂叶薯目前尚未形成入侵危害,而裂叶牵牛在华南地区展现出一定的入侵性^[7](也有学者认为裂叶牵牛为非入侵植物^[8])。本研究以五爪金龙、裂叶牵牛和三裂叶薯这3种在华南地区具有不同入侵性的近缘植物作为研究对象,通过测定和比较它们在低温胁迫下的生理生态响应,探究这3种植物的低温敏感性与入侵性之间的关系。我们提出以下两个假设:(i)五爪金龙、裂叶牵牛以及三裂叶薯对低温胁迫具有较高的敏感性;(ii)严重入侵植物五爪金龙的低温敏感性要低于非入侵植物(或轻度入侵植物)三裂叶薯和裂叶牵牛。

1 材料与方法

1.1 试验材料与处理

选取华南地区野外相似生境中五爪金龙、裂叶牵牛和三裂叶薯的自然种群,分别剪取3种植物的成熟茎段,于3 h之内带回实验室,并放置于自来水中不超过12 h。分别剪取10 cm带两个腋芽且不带分枝的茎段,用Hoagland营养液进行水培。经4周预培养后,选取生长健壮、长势一致的植株分别放入不同培养箱水培,并进行不同温度处理。考虑到五爪金龙在华南形成入侵的区域1月平均气温通常在10 °C以上,本研究的低温处理组设置为15 °C和10 °C两组,对照组为28 °C,昼夜温度一致,处理

时间为8 d。每种植物每个处理种植9株作为重复;培养箱光照周期为12 h,光照强度为 $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ 。

1.2 测试与分析

在低温处理期间,每隔两天用PAM-2100(Walz,德国)进行叶绿素荧光参数的测定。活体全叶叶片检测时先用测量光($0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$)测定初始荧光 F_0 ,饱和光脉冲 $2700 \mu\text{mol m}^{-2} \text{s}^{-1}$ (脉冲时间0.8 s)诱导 F_m ,光化光强度为 $186 \mu\text{mol m}^{-2} \text{s}^{-1}$ 。测量前将活体植株置于暗箱内适应30 min,选取完全展开的第5—7叶片,每片叶选取2个圆形区域进行测定。本研究重点关注能够反映光合系统II(PS II)活性的初始荧光强度(F_0)、最大原初光能转换效率(F_v/F_m)、最大电子传递速率(ETR),以及反映植物热耗散能力的PS II非光化学淬灭系数(NPQ)。植物收获时,用称重法测定植物新增枝条的生物量。对于植物叶片,采用二氨基联苯染色法检测低温诱导后的 H_2O_2 积累;参照李合生^[9]的方法测定丙二醛(MDA)和脯氨酸含量;采用蒽酮比色法测定可溶性糖含量。对于植物根系,采用拍照-Image J软件计算的方法测定根长;用氯化三苯基四氮唑法测定根系活力,用Evans Blue染色-分光光度法测定根尖细胞细胞膜的完整性。

1.3 统计分析

采用SPSS 16.0软件进行数据处理,运用最小显著差数法(LSD)进行处理效应的显著性分析。用OriginPro 8.0软件作图。

2 结果与分析

2.1 不同温度处理下3种植物的再生枝条生物量及根长

如图1所示,15℃和10℃的低温处理均极显著的降低了3种植物新生枝条生物量的积累以及根系的生长($P<0.01$)。在15℃低温处理下,与对照组相比3种植物再生枝条生物量的积累减少了60%以上,植物的根长也减少85%以上。在10℃处理下,三裂叶薯和牵牛基本已停止生长,五爪金龙新生枝条生物量及相对根长与对照组相比分别减少了78.3%和92.0%。这些结果表明,3种植物地上、地下部的生长均对低温较为敏感,并且五爪金龙对低温的敏感性要明显低于三裂叶薯和裂叶牵牛。

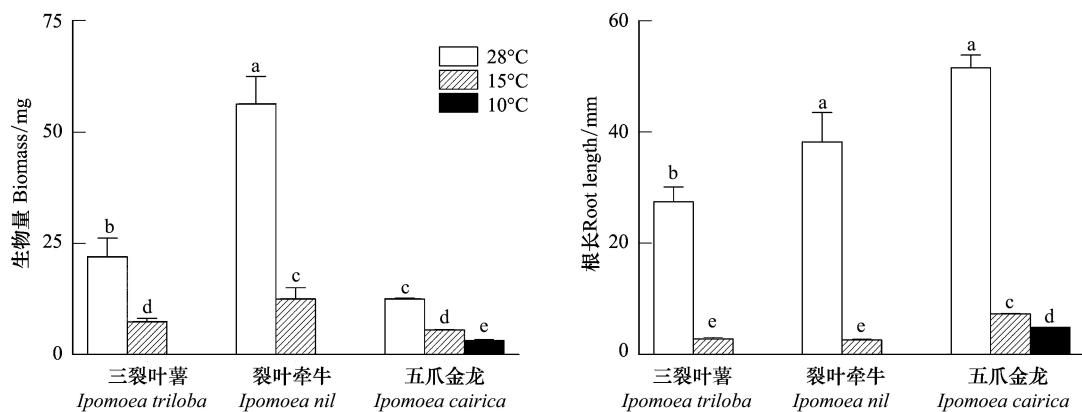


图1 低温处理(15°C 和 10°C)对外来植物三裂叶薯、裂叶牵牛和五爪金龙地上部生物量及根长的影响

Fig.1 Effects of low temperature treatments (15°C and 10°C) on shoot biomass and root length of the alien plants *I. triloba*, *I. nil* and *I. cairica*

不同字母表示在0.05水平差异显著

2.2 不同温度处理下3种植物叶片的渗透调节物质含量

如图2所示,15℃低温处理8 d后三裂叶薯和裂叶牵牛叶片中的脯氨酸和可溶性糖含量均有极显著的增加($P<0.01$);五爪金龙叶片中的脯氨酸浓度以及可溶性糖含量也有显著的增加($P<0.05$),不过增加幅度均要明显低于裂叶牵牛和三裂叶薯。脯氨酸和可溶性糖是植物体内主要渗透调节物质。不少研究发现,植物在感受到低温胁迫时会通过积累脯氨酸、可溶性糖等渗透调节物质来提高细胞、组织的冰点温度,进而为关键酶、抗逆性蛋白和生物膜等提供保护^[10-11]。本实验的研究结果表明,15℃的温度条件对3种植物(尤其是三裂叶薯和裂叶牵牛)已经造成了明显的低温胁迫,使得三者通过大量积累脯氨酸和可溶性糖来加强对自身保护。

2.3 不同温度处理下3种植物叶片的 H_2O_2 和丙二醛含量

如图3所示,未经低温处理的三裂叶薯、裂叶牵牛和五爪金龙的叶片均无明显的黄色沉淀,且颜色大致相同,表明它们叶片中的 H_2O_2 的含量保持在较低水平。经过15℃低温处理8 d后,3种植物叶片中均积累了较多 H_2O_2 ,而且三裂叶薯叶片中的 H_2O_2 量要明显高于五爪金龙和裂叶牵牛。同时,经过15℃低温处理后,三裂叶薯、裂叶牵牛和五爪金龙叶片的MDA含量相比对照组均有显著的增加($P<0.05$),增加幅度分别为35%、122%和90%。低温胁迫导致植物体内过氧化物的积累以及MDA含量的增加已有不少报道^[12]。本研究的结果表明,低温处理同样引起了3种番薯属植物叶片中过氧化物的积累,进而导致植物细胞膜脂过氧化。

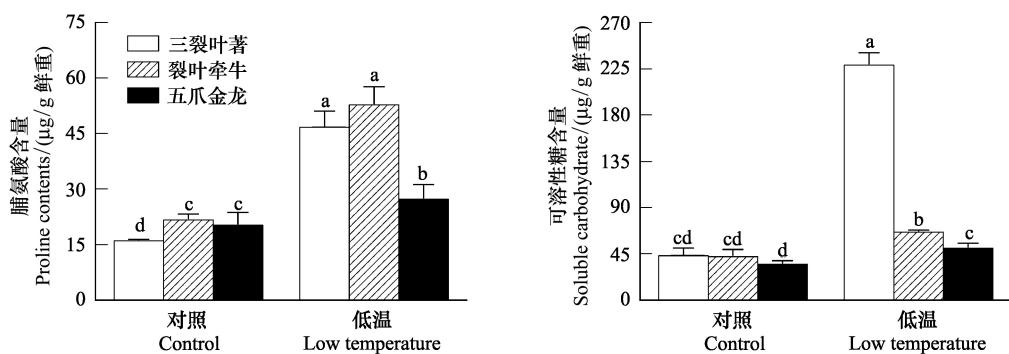


图 2 低温(15 °C)处理对外来植物三裂叶薯、裂叶牵牛和五爪金龙的脯氨酸和可溶性糖含量的影响

Fig.2 Effects of low temperature treatment (15 °C) on the contents of proline and soluble carbohydrate in the leaves of alien plants *I. triloba*, *I. nil* and *I. cairica*

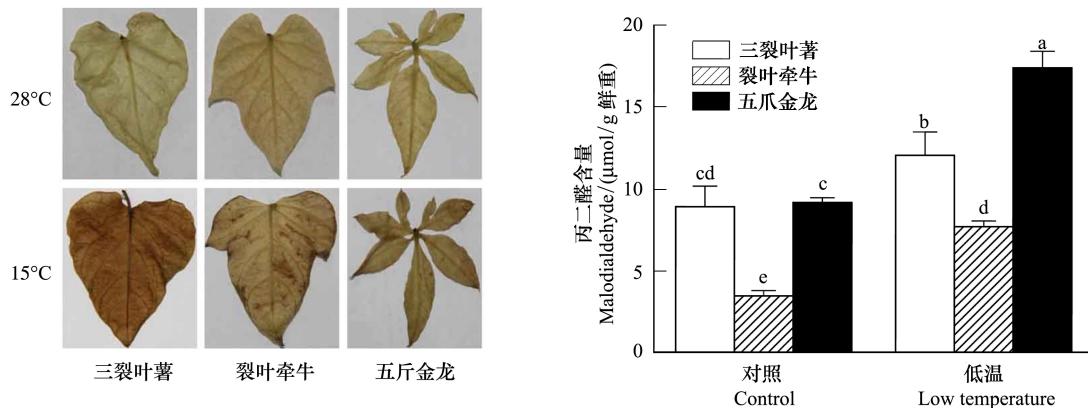


图 3 低温(15 °C)胁迫对外来植物三裂叶薯、裂叶牵牛和五爪金龙叶片中 H_2O_2 和丙二醛含量的影响

Fig.3 Effect of low temperature treatment on the contents of H_2O_2 and malondialdehyde in leaves of the alien plants *I. triloba*, *I. nil* and *I. cairica*

染色剂:二氨基联苯染色

2.4 不同温度处理下3种植物的叶绿素荧光特征

F_0 是PS II反应中心全部开放(即 Q_A 全部氧化)时的荧光水平。PS II反应中心的破坏或可逆失活通常会引起 F_0 的增加^[13]。 F_v/F_m 反映的是PS II反应中心原初光能转化效率及PS II反应中心潜在活性。当植物处于正常条件下时,该参数一般为0.76—0.85^[13],但在逆境或遭受伤害时会明显下降。如图4所示,在15 °C低温处理下,随着处理时间的延长三裂叶薯的PS II反应中心受到的损伤逐渐增大(表现为 F_0 呈现明显的上升趋势,而 F_v/F_m 则明显下降)。裂叶牵牛和五爪金龙叶片的PS II反应中心也受到一定破坏,但是损伤程度要明显低于三裂叶薯。

ETR也能反映PS II反应中心的活性,它与植物的光合速率有很强的线性关系^[14]。随着低温处理时间的延长,3种植物的ETR均表现出下降的趋势。15 °C低温处理8 d之后,三裂叶薯、牵牛和五爪金龙的ETR相比对照组分别下降了12.9%、7.4%和13.7%。NPQ表示的是植物捕光色素吸收光能后以热的形式耗散过剩激发能的能力,热耗散是植物保护PS II的重要机制^[15]。随着低温处理时间延长,3种植物的NPQ呈现上升的趋势,表明它们启动热耗散来消耗过量的激发能,以减轻低温胁迫下过量光能对光合结构的损伤。低温处理8 d后,三裂叶薯、裂叶牵牛和五爪金龙的NPQ分别上升了44.0%、69.1%和229.5%,表明五爪金龙热耗散能力要明显优于另外2种植物。

2.5 不同温度处理下3种植物根系活力以及细胞膜完整性

为了探测低温对三裂叶薯、牵牛和五爪金龙3种植物根系细胞的细胞膜透性的影响,用Evans Blue染色剂作为细胞膜透性变化的指示剂。如图5所示,与对照组相比,三裂叶薯、裂叶牵牛和五爪金龙根系的细胞膜透性均有极显著的增加($P<0.01$),增加幅度分别为83%、428%和53%。说明低温严重破坏了3种植物根细胞膜的完整性,从而导致根部细胞的死亡。与三裂叶薯和裂叶牵牛相比,五爪金龙的根系细胞死亡率较低,说明其耐寒性要强于裂叶牵牛和三裂叶薯。

根系活力一般与植物的吸收、合成、氧化和还原等能力有关,它可以反映植物根系的生理活性以及植物的呼吸强度。本研

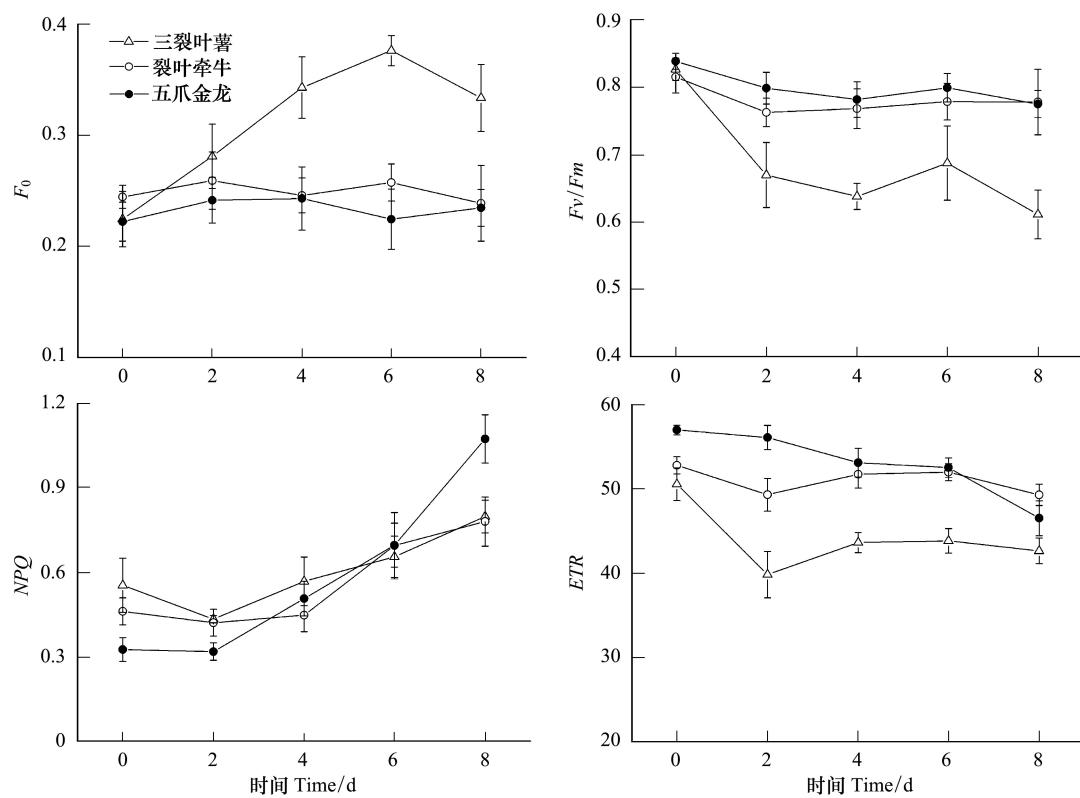


图4 低温胁迫下外来植物三裂叶薯、裂叶牵牛和五爪金龙叶片叶绿素荧光参数的动态变化

Fig.4 The dynamics of chlorophyll fluorescence parameters in leaves of alien plants *I. triloba*, *I. nil* and *I. cairica* under low temperature stress

F_0 :初始荧光强度, F_v/F_m :最大原初光能转换效率, ETR:最大电子传递速率, NPQ:非光化学淬灭系数

究以对氯化三苯基四氮唑还原量(即呼吸强度)来表征植物的根系活力。结果表明(图5),与对照组相比,经过15℃低温处理后,3种植物单位根重的根系活力比对照组分别增强了约7.1倍、6.8倍和19.6倍。在10℃低温处理组,五爪金龙的根系活力依然比对照组高6.5倍,但是裂叶牵牛和三裂叶薯的根系活力相比对照组有所下降。由于在15℃和10℃的低温处理下植物的根系生长均受到强烈抑制,且部分根细胞出现死亡,植物根系活力的大幅提高可能是通过极大提高根内活细胞的呼吸强度实现的;这应该是植物对根系功能的一种补偿效应。弋良朋等^[16]发现3种植荒漠盐生植物的根系在较高的盐胁迫处理下也有类似的表现。不过,在10℃处理下,裂叶牵牛和三裂叶薯的这种补偿效应已经不复存在,表明在此温度下两种植物根系的功能已严重受损。结合它们地上部生物量的数据,可以推测10℃已经接近裂叶牵牛和三裂叶薯的耐受极限。

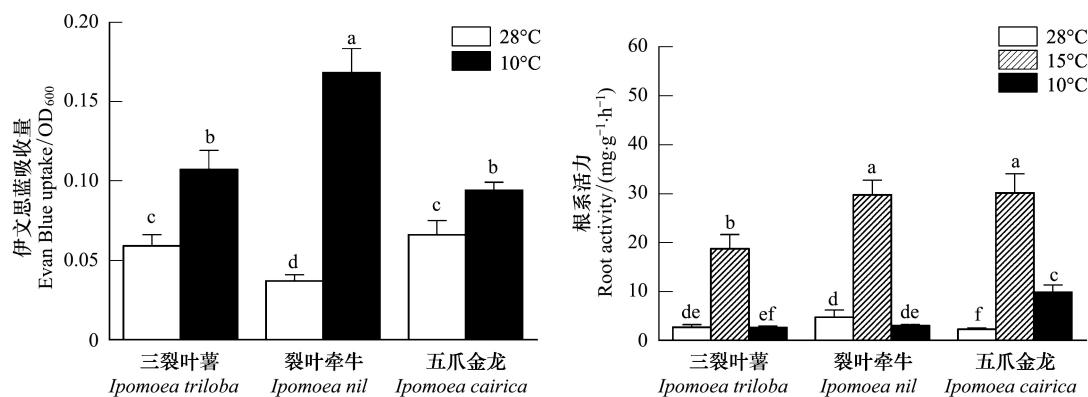


图5 低温对外来植物三裂叶薯、裂叶牵牛和五爪金龙细胞膜完整性和根系活力的影响

Fig.5 Effect of chilling on the membrane integrity and the root activity of the alien plants *I. triloba*, *I. nil* and *I. cairica*

3 讨论

植物的光合作用是对低温胁迫较为敏感的生理过程^[17]。这是由于低温胁迫会导致植物体内与光合作用相关酶类(如核酮糖二磷酸羧化酶)失活或降解,进而损伤植物的光合系统^[18]。此外,低温导致的活性氧自由基的积累也会对光合系统产生损害^[19]。在本研究中,15℃的温度处理下3种番薯属植物均启动热耗散来消耗过量的激发能(表现为NPQ升高),以减轻过量光能对光合结构的损伤。但是,15℃的低温处理对它们的光合系统仍然造成了损伤,导致3种植物PSⅡ活性出现不同程度的降低(表现为F₀升高,F_v/F_m、ETR降低)。这与不少其它植物在遭受低温处理下的响应方式类似^[19]。相比之下,三裂叶薯光合系统的损伤程度要明显高于五爪金龙和裂叶牵牛,表明其光合系统对低温更为敏感。

低温胁迫能够强烈影响植物的各项生理活动,要客观反映植物的低温敏感性需要综合观测与植物耐(抗)寒性相关的各项生理指标^[12,20]。本研究为了简化试验条件,植物栽培采用水培的方式,温度设置则采取昼夜温度一致的处理,这与自然条件下相差较大。不过作为模拟试验,本研究对于揭示温度对3种植物入侵性、分布区域的影响仍然具有积极的意义。通过测定在不同温度处理下植物的生物量、活性氧、渗透调节物质、根系活力、光合特征等生理指标发现,在15℃处理下3种植物的叶片中已经积累了较高浓度的活性氧(H₂O₂)。这些活性氧的积累一方面引起细胞膜损伤,导致丙二醛在植物体内的累积,另一方面还对植物的光合系统产生了破坏,并严重抑制了植物地上、地下部的生长。这些结果清晰地表明,15℃的温度条件已经能够对3种番薯属植物形成较为强烈的胁迫作用,进而支持了本研究的第一个假设,即五爪金龙、裂叶牵牛以及三裂叶薯具有较高的低温敏感性。由于入侵植物广泛的生态、生理适应性是其入侵性形成的动力基础^[21-22],这种对低温较高的敏感性很可能是限制它们在我国华南以外的地区形成入侵危害的重要原因。

探究物种分布的限制性因素一直是生态学研究中重要的科学问题^[23],尤其是在全球气候变化受到极大关注的背景下^[22]。近年来,全球气候变化导致非本土植物分布区扩张的现象引起了众多学者的注意^[24-25]。Bijoor等^[26]通过在野外开展的模拟增温实验发现,温度增加可能会提高部分植物(尤其是C4植物)的入侵性。Wang等^[27]通过比较五爪金龙在不同温度(22, 26, 30℃)下的种子萌发速率、生物量积累与分配模式以及化感强度之后提出,全球气候变暖可能会加速五爪金龙的入侵。因此,尽管目前尚未发现五爪金龙在华南以外的地区形成入侵危害,在全球气候变暖的背景下需要密切监测其可能出现的生境扩张现象。

综合比较五爪金龙、三裂叶薯和裂叶牵牛在低温胁迫下生物量积累、光合特征、根系活力等生理特征的响应强度发现,尽管它们对低温胁迫均较为敏感,3种近缘植物之间的低温敏感性存在一定的差异。在10℃的低温胁迫下,只有五爪金龙能够继续生长,表明其对低温的耐受性高于三裂叶薯和裂叶牵牛,进而支持了本研究的第2个假说,即严重入侵植物五爪金龙的低温敏感性要低于非入侵植物(或轻度入侵植物)三裂叶薯和裂叶牵牛。此外,在低温胁迫下三裂叶薯体内积聚的过氧化物浓度(H₂O₂)最高,且光合系统Ⅱ受损也最为严重,表明其对低温的耐受性最低。3种植物对低温胁迫的耐受性由高到低依次为:五爪金龙>裂叶牵牛>三裂叶薯。外来植物入侵是非常复杂的生态学过程,是外来植物与入侵地各种生物、非生物因素综合作用的结果^[28]。决定外来植物能否入侵及其入侵能力大小的因素很多^[29],既包括植物自身拥有的入侵性性状,也包括入侵地的可入侵性。Bykova等^[30]比较了在北美洲西部半干旱地区形成严重入侵危害的旱雀麦(*Bromus tectorum*)和红雀麦(*Bromus rubens*)对低温的耐性,发现旱雀麦幼苗的耐冻能力要强于红雀麦幼苗,进而导致旱雀麦能够在北美洲西北部造成更为严重的入侵性危害。本研究中,五爪金龙、三裂叶薯以及裂叶牵牛对低温的耐受性与它们在华南地区造成的入侵危害程度表现一致,说明低温敏感性的差异可能是它们在华南地区入侵性差异的重要原因之一。

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