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木榄和秋茄对水渍的生长与生理反应的比较研究

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摘要:研究了不同水渍时间对两种红树植物木榄(*Bruguiera gymnorrhiza* (L.) Lam)和秋茄(*Kandelia candel* (L.) Druce)的生长与生理的影响。随着淹水时间的增加,木榄的相对生长率明显减小;排水处理的木榄相对生长率最大而淹水时间最长(12 周)的植物具有最低的生长率。相反,淹水与排水处理对秋茄的相对生长率的影响并无显著差异。在生物量的分配即茎根比(*S/R* 值)上,这两种植物亦表现出对水渍的不同反应。较长淹水时间(8 周或 12 周)处理组的秋茄具有较高的 *S/R* 值,但各处理间木榄 *S/R* 值无显著变化。由此看出,随着淹水时间的延长,秋茄生物量分配从根部向地上部转移,而木榄却无这种变化。12 周淹水处理的秋茄具有比排水处理组更高的根系活力,而所有淹水处理组的木榄的根系活力均低于排水处理的值。这些差异表明,木榄比秋茄对水渍更敏感。淹水处理中秋茄基本上比木榄具有更高的硝酸盐还原酶、过氧化物酶及超氧化物歧化酶活性,这进一步说明秋茄比木榄对水渍有更强的耐受力。但在叶片叶绿素和胡萝卜素含量上,两种植物对水渍有类似的反应:淹水处理比排水处理有更高的光合色素含量。

关键词:木榄;秋茄;水渍;生长;生理

Studies on differences in growth and physiological responses to waterlogging between *Bruguiera gymnorrhiza* and *Kandelia candel*

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Abstract: Effects of different waterlogged time on growth and physiological responses of two mangrove species, *Bruguiera gymnorrhiza* and *Kandelia candel*, were investigated. Mature propagules of *K. candel* and *B. gymnorrhiza* were collected at Mai Po Mangrove Nature Reserve in Hong Kong in March and April 1997, respectively. Four propagules were planted in a plastic pot containing 4 kg soils collected from the same mangrove forest. On 14 October 1998, 4 *B. gymnorrhiza* pots and 4 *K. candel* pots were selected as materials for the waterlogged experiment. For each species, 4 treatments were set up to examine the growth and physiological responses to 4 waterlogged times, that is, drained for 12 weeks (D), drained for 8 weeks + waterlogged for 4 weeks (W4), drained for 4 weeks + waterlogged for 8 weeks (W8), and waterlogged for 12 weeks (W12). During drained periods, each pot was put onto a shallow tray (3 cm deep) and irrigated with 400 ml artificial seawater (salinity of 15) every two days, in the same way as previously described. For waterlogged treatments, each pot was placed inside a plasic container full of artificial seawater to ensure that the pot was waterlogged and the soil surface was inundated with 5 cm seawater.

At the beginning of the experiment, all pots had similar redox potentials as the soils were drained

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before. The soil redox potentials of *B. gymnorrhiza* pots and *K. candel* pots were-14 and -8mv, respectively. At the end of the experiment, soil redox potentials decreased significantly with waterlogged time, in the descending order of D $>$ W4 $>$ W8 $>$ W12 for both *B. gymnorrhiza* and *K. candel* pots. This indicates that continuous waterlogging resulted in oxygen-deficiency in mangrove soils. The redox potentials of *K. candel* pots were less negative than those in *B. gymnorrhiza* pots, suggesting that *K. candel* plants may transport more oxygen through aerial parts to roots then to soil than *B. gymnorrhiza* plants. From this, it seems that *K. candel* may have more tolerance to waterlogging than *B. gymnorrhiza*, which will be further tested by their different responses to waterlogging on growth and physiology as follows.

Growth responses, in terms of biomass partitioning and relative growth rath, to waterlogging were different between the two species. Generally *K. candel* had lower shoot/root biomass ratio(S/R) than *B. gymnorrhiza*. For *B. gymnorrhiza*, no significant differences were found in S/R among the four treatments. For *K. candel*, S/R was low in drained (D) plants when compared to plants subjected to 8-weeks(W8) or 12-weeks(W12) waterlogged treatments, suggesting that more biomass were allocated to shoots than roots under prolonged waterlogging in *K. candel*.

The relative growth rate(*RGR*) was not significantly different among four treatments in *K. candel* but the *RGR* dropped significantly with waterlogged time in *B. grmnorrhiza*. The *RGR* of *B. gymnorrhiza* was higher than that of *K. candel* if the plants were drained or were waterlogged for less than 8 weeks. However, in the 12-weeks waterlogged treatment (W12), there was no significant difference in *RGR* between *K. candel* and *B. gymnorrhiza*. According to two-way ANOVA, a very significant interaction was found between species and treatment, implying that these two species responded differently to waterlogging in growth.

The interaction between species and treatment in terms of root activity measurement was significant, indicating the two species had different responses to waterlogging. Root activity of *B. gymnorrhiza* subjected to 12-weeks waterlogging(W12) declined significantly when compared to the drained(D), W4 and W8 plants. On the contrary, the highest root activity was found in *K. candel* plants with prolonged waterlogging, the activity in W12 treated plants were significantly higher than the drained plants which had similar activity as the plants subjected to 4 or 8 weeks waterlogged treatments.

The concentrations of chlorophyll a, chlorophyll b and total carotenoids in W8 and/or W12 treated *B. gymnorrhiza* and *K. candel* were significantly higher than the respective drained (D) or W4 plants. This suggests that mangrove plants had an increase in photosynthesis under prolonged waterlogging. No significant interaction was found between species and treatment for chlorophyll a, chlorophyll b and total carotenoid contents, indicating that both plant species had similar photosynthetic response to waterlogging.

Both species had higher nitrate reductase(NR) activity in leaf and stem than in root. For NR activity, interaction between species and treatment was very significant in root but not so in leaf and stem, indicating that *B. gymnorrhiza* responded to waterlogging by means of root NR activity were different from *K. candel*. For each component of each species significant differences in NR activity were found among 4 treatments. NR activity in leaf and stem of both species tended to increase with waterlogged time. The highest root NR activity was found in W12 treated *B. gymnorrhiza* but prolonged waterlogging did not cause any significant increase in *K. candel*.

The peroxidase activities in leaf, stem and root were significantly different between species, but no significant interaction was found between species and treatment. The activities in *K. candel* were significantly higher than in *B. gymnorrhiza*, and the activity changed very little in the former species when subjected to waterlogging. In leaf and root of *B. gymnorrhiza*, peroxidase activities were significantly

different among treatments and higher when they were waterlogged for 12 weeks than the other treatments.

Both *B. gymnorrhiza* and *K. candel* showed similar responses in superoxide dismutase (SOD) activity to waterlogging as the interaction between species and treatment in all measurements of SOD activity was not significant. SOD activity was significantly higher in *K. candel* than in *B. gymnorrhiza*, and waterlogging had no significant effect on this activity in leaf, stem and root of *K. candel*. On the other hand, higher activities were found in root and stem of *B. gymnorrhiza* receiving 12-weeks waterlogged treatment.

Key words: *Bruguiera gymnorrhiza*; *Kandelia candel*; waterlogging; growth; physiology

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分布于热带亚热带海岸潮间带的红树林正面临着全球海平面上升的严峻挑战[1]。近年来的研究还表明,红树林可用作废水的天然处理厂[2]。海平面上升和废水排入均将使红树林的水渍时间增加从而影响其生长和生理过程。尽管红树植物被视为耐水淹种类[3],但主要对西方红树林类群中 3 个物种的水渍反应有过一些报道[4]。这些研究主要集中于大红树(*Rhizophora mangle*)、亮叶白骨壤(*Avicennia germinans*)及假红树(*Laguncularia racemosa*)的光合速率、水分代谢和根系呼吸等方面对水渍的反应。Naidoo 研究了水渍对 3 种东方类群的红树植物白骨壤(*Avicennia marina*)、红茄冬(*Rhizophora mucronata*)和木榄叶绿体、组织水势及离子含量的影响[5]。一些对非红树植物的研究表明,水渍对植物营养盐利用与吸收及活性氧的产生均有影响[6,7]。

木榄(*Bruguiera gymnorrhiza* (L.) Lam)和秋茄(*Kandelia candel* (L.) Druce)是我国东南部海岸的两种主要红树植物。有关其对水渍的反应及耐受性极少有报道,但在野外观察中得知秋茄自然分布的滩面较木榄低[8]。本研究的目的是比较这两种红树植物在生长和生理上对不同淹水时间的反应。利用同一物种不同淹水时间生物量和相对生长率(*RGR*)的差异为指标来指示植物生长对水渍的反应。在其它红树植物和非红树植物中,这两个参数被视为重要的耐水渍指标[1,4,5,9]。还测定了根系活力、叶片光合色素含量以及硝酸盐还原酶、过氧化物酶及超氧化物歧化酶活性,以探索水渍对根系呼吸、光合作用、营养盐利用以及抗氧化作用等生理过程的影响。

1　材料与方法

分别于 1997 年 3 月和 4 月从香港米埔红树林自然保护区采集秋茄和木榄的成熟繁殖体。每 4 个繁殖体种植于一盛 4 kg 米埔红树林土壤的塑料盆(直径 18 cm 高 20 cm)中。将这些植物放置于温室(25±5 ℃)内,在开始试验前各盆每 2 天浇 400 ml 盐度 15 的人工海水(用速溶海盐与自来水配制而成)。塑料盆底部有 6 个排水孔。于 1998 年 10 月 14 日选取 4 盆木榄和 4 盆秋茄作为水渍试验的材料。所选木榄的基径和高度分别为 0.78±0.11 cm 和 23.1±3.7 cm(n=16),秋茄的基径和高度分别为 0.73 ± 0.07 cm 和 30.5 ± 4.2 cm(n=16)。

1.1　试验设计

两种植物均设置 4 个处理:排水 12 周(D);排水 8 周+淹水 4 周(W4);排水 4 周+淹水 8 周(W8);淹水 12 周(W12)。W12、W8 和 W4 的淹水处理分别开始于 1998 年 10 月 14 日、11 月 11 日和 12 月 9 日,所有处理均在 1999 年 1 月 7 日结束。在排水处理期间,各盆均如试验前一样每两天浇以 400 ml 盐度 15 的人工海水。淹水处理时将试验盆置于大塑料容器(长 30 cm、宽 40 cm、高 30 cm)中,该容器盛盐度 15 的人工海水使植物盆一直保持 5 cm 的淹水深度。每日添加自来水补充容器内蒸发的水分使容器水位不变。容器内的人工海水每周换 1 次以确保水质不被腐化。于 1999 年 1 月 7 日即所有处理结束时收获所有植物测量和分析每株植物的生长和生理参数。由于植物数量上的限制,各处理仅设一个植物盆,同一盆内的 4 株植物视为 4 个重复而分别测定有关参数。

1.2　土壤氧化还原电位和植物生长分析

处理结束时在各盆土壤的 3 个随机位点插入铂电极,插入深度为 5 cm,平衡 30 min 后读取土壤氧化

还原电位值。

在试验开始和结束时分别测量各植株的基径(D,在茎的第 1 节处量取)和高度(H,除胚轴外的茎长)。试验结束时将各植株分为地上部(叶和茎)和根部,洗净后在 105 ℃烘干至恒重以分析生物量分配。由于在试验期间胚轴的重量无变化,测定地上部和根部生物量时均不包括胚轴部分。试验结束时各植株的总生物量(B)、基径(D)和高度(H)采用 Snedaker 和 Snedaker 建议的方程来拟合[10]。所得关系式如下:

$$\text{木榄}\quad \log B = 0.6439 + 0.3053 \log (D^2H) \quad (n = 16,\ p < 0.05)$$

$$\text{秋茄}\quad \log B = 0.3353 + 0.5111 \log (D^2H) \quad (n = 16,\ p < 0.05)$$

最初的生物量由上述方程估算。相对生长率(RGR)则由下式计算:

$$RGR = (\log B_2 - \log B_1)/(t_2 - t_1)$$

其中 B_1 和 B_2 分别为试验开始时(t_1)和结束时(t_2)的总生物量[11]。

1.3 生理参数分析

称取约 0.1 g 第 3 对叶的新鲜组织于冰浴中用 10 ml 80%的丙酮研磨。匀浆液于 10000×g 离心 3 min。按照 Lichtenthaler 和 Wellburn 的方法测定叶绿素 a、叶绿素 b 和总胡萝卜素含量[12]。根系活力的测定与张志良描述的方法类似并略作改进[13]。取 0.3 g 新鲜植物组织(成熟叶、顶节茎及根尖)按 Ross 的方法测定硝酸盐还原酶活性,并略作改进[14]。过氧化物酶与超氧化物歧化酶活性的测定按刘祖祺和张石城的方法[15]。

1.4 数据处理

计算 4 个重复的平均值和标准误差。采用双因素方差分析(2-way ANOVA)以物种与淹水处理为因素检验两种植物间对水渍反应的差异、同一物种各处理间的差异以及物种与处理间的相互作用。如存在显著差异的话,采用 Student-Newman-Keuls 多项比较法检验差异的显著性。

2 结果

2.1 土壤氧化还原电位

试验开始前均为排水处理,各植物盆试验开始时有类似的土壤氧化还原电位。木榄盆的土壤氧化还原电位为 -14 ± 2 mv($n=4$),秋茄盆为 -8 ± 1 mv($n=4$)。试验结束时,土壤氧化还原电位随淹水时间增加而减小,其值大小排序均为 D>W4>W8>W12(图 1)。这说明连续的淹水导致了盆内土壤的缺氧。秋茄土壤氧化还原电位值较木榄土壤高,说明秋茄植物体由通气组织向根系和土壤传输氧的能力比木榄强。由此可知,秋茄可能比木榄对水渍有更强的耐受力,这一点还将从下文中的生长和生理反应得以证实。

2.2 生长反应

在生物量分配和相对生长率两个指标上,木榄和秋茄对水渍有不同反应(图 2)。普遍来说,秋茄比木榄具有较低的 S/R 值。木榄的 S/R 值在 4 个处理间不存在显著差异(图 2、表 1)。对于秋茄而言,排水处理组(D)比淹水 8 周(W8)和 12 周(W12)的处理组具有较低的 S/R,说明在一定的水渍期间内秋茄生物量向根部转移。

秋茄相对生长率(RGR)在各处理间无显著差异,但木榄的 RGR 值随着淹水时间的增加而减小(图 2 和表 1)。排水组和淹水时间少于 8 周的处理组中,木榄比秋茄具有较大的 RGR 值。然而,淹水 12 周的处理组两种植物的 RGR 值相似。根据双因素方差分析发现物种与处理间存在显著的相互作用,说明这两种植物对水渍有不同的生长反应(表 1)。

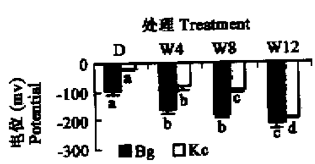

图 1 木榄(Bg)和秋茄(Kc)盆土壤氧化还原电位

Fig. 1 Soil redox potentials of *B. gymnorrhiza* (Bg) and *K. candel* (Kc) pots

2.3 生理反应

从根系活力的测定结果来看,物种和处理间存在相互作用(表 1),说明两种植物对水渍有不同的反应。

淹水 12 周处理组的木榄根系活力显著低于排水组、淹水 4 周组和淹水 8 周组(图 3 和表 1)。相反，秋茄根系活力的最大值出现在较长淹水处理时间组即淹水 12 周组(图 3)。

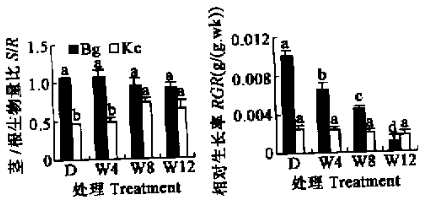

图 2 木榄(Bg)和秋茄(Kc)生长对水渍的反应

Fig. 2 Growth responses of *B. gymnorrhiza*(Bg) and *K. candel* (Kc) to waterlogging

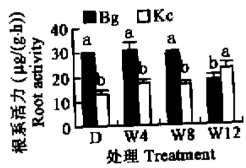

图 3 木榄(Bg)和秋茄(Kc)根系活力对水渍的反应

Fig. 3 Responses of root activity of *B. gymnorrhiza*(Bg) and *K. candel*(Kc) to waterlogging

光合色素(叶绿素和胡萝卜素)随淹水处理时间的变化见图4。淹水8周和/或12周的木榄和秋茄明显比排水和淹水4周的处理组具有更高的叶绿素a、叶绿素b和胡萝卜素含量(图4和表1)。这说明这两种红树植物在一定的淹水时间内光合作用增强。在叶绿素a、叶绿素b和胡萝卜素含量这些指标上物种与处理间无显著差异(表1),说明在光合作用方面,两种植物对水渍的反应相似。

两种植物的叶和茎硝酸盐还原酶活性均高于根部的值(图5)。根部硝酸盐还原酶活性存在物种和处理间的相互作用,但在叶和茎部则不存在这种相互作用(表1),说明木榄的根系硝酸盐还原酶活性对水渍的反应与秋茄明显不同。各物种各组分中硝酸盐还原酶活性在4个处理间有显著差异(表1)。两种植物的叶片和茎硝酸盐还原酶活性均有随淹水处理时间增加而增加的趋势。木榄根系硝酸盐还原酶活性最大值出现在淹水12周处理组,但淹水处理时间的增加并不导致秋茄根系硝酸盐还原酶活性的增强。

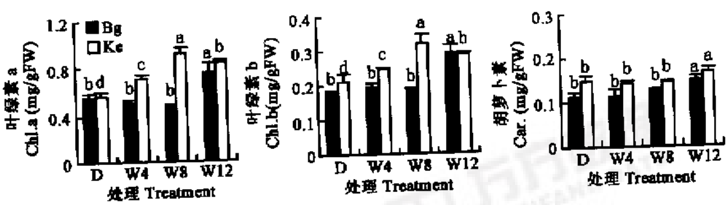

图 4 木榄(Bg)和秋茄(Kc)光合色素(叶绿素和胡萝卜素)含量对水渍的反应

Fig. 4 Responses of chlorophyll (chl.) and carotenoid (car.) contents in *B. gymnorrhiza* (Bg) and *K. candel* (Kc) to waterlogging

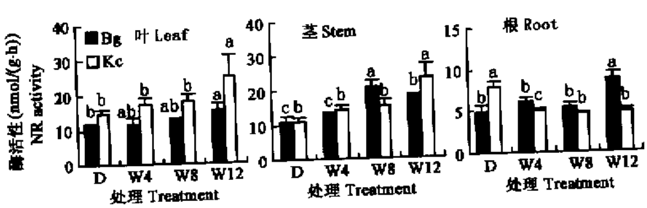

图 5 木榄(Bg)和秋茄(Kc)叶、茎、根硝酸盐还原酶活性对水渍的反应

Fig. 5 Responses of nitrate reductase (NR) activity in leaf, stem and root of *B. gymnorrhiza* (Bg) and *K. candel* (Kc) to waterlogging

表 1　双因素方差分析结果

Table 1　Results of 2-way ANOVA

指标 Indicators	差异来源 Source of variation			比较 Comparison	
	物种(S) Species	处理(T) Treatment	S×T	木榄 *B. gymnorrhiza*	秋茄 *K. candel*
茎/根比 *S/R*	91.65***	0.48	4.85*	3.38	10.03***
相对生长率 *RGR*	28.01***	12.36***	9.62**	144.80***	1.62
根系活力 Root activity	29.44***	0.29	4.38*	22.17***	13.56***
光合色素 Photosynthetic pigment					
叶绿素 a Chl. a	11.40***	13.78***	1.80	26.51***	53.83***
叶绿素 b Chl. b	6.10*	9.03**	0.66	34.85***	21.11***
胡萝卜素 Car.	16.36***	1.83	1.08	9.28*	5.76*
硝酸盐还原酶活性 Nitrate reductase activity					
叶 Leaf	10.44***	4.57*	1.30	4.53*	5.50*
茎 Stem	0.01	11.54	0.00	30.90***	13.53***
根 Root	1.83	0.31	14.57***	19.39***	44.72***
过氧化物酶活性 Peroxidase activity					
叶 Leaf	12.84***	3.68	2.99	6.58*	7.65**
茎 Stem	38.90***	0.38	0.11	2.95	2.87
根 Root	76.36***	3.59	0.63	7.59**	1.34
超氧化物歧化酶活性 Superoxide dismutase activity					
叶 Leaf	22.34***	0.16	0.09	0.45	1.07
茎 Stem	20.81***	0.45	1.52	6.16*	3.10
根 Root	21.36***	5.70*	2.41	10.22***	0.38

F 值的显著性　*F*-values are given and significant effects: * 0.05; ** 0.01; *** 0.005

两种植物间叶、茎和根的过氧化物酶活性具有显著差异,但并不存在物种和处理间的相互作用(表 1)。秋茄的过氧化物酶活性显著高于木榄的值,且淹水并不导致秋茄过氧化物酶活性的明显变化。在叶和茎中,木榄过氧化物酶活性在各处理间有显著差异(表 1),淹水 12 周处理组比其它处理组的值均要高(图 6)。

木榄和秋茄的超氧化物歧化酶活性对水渍表现出类似的反应(表 1)。秋茄的超氧化物歧化酶活性明显比木榄高,且淹水对秋茄叶、茎和根酶活性均无显著影响(图 7 和表 1)。12 周淹水处理的木榄超氧化物歧化酶活性在根和茎部较高。

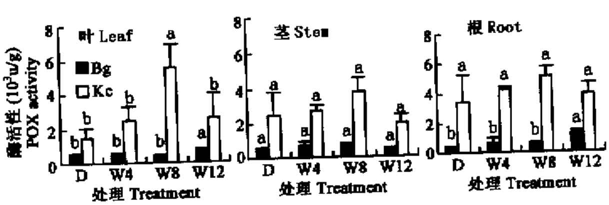

图 6　木榄(Bg)和秋茄(Kc)叶、茎、根过氧化物酶活性对水渍的反应

Fig. 6　Responses of peroxidase (POX) activity in leaf, stem and root of *B. gymnorrhiza* (Bg) and *K. candel* (Kc) to waterlogging

3　讨论

3.1　生长与生物量分配对水渍的反应

水渍使得木榄和秋茄的土壤氧化还原电位减小(图 1),即导致土壤缺氧。然而,就同一处理而言,秋茄盆比木榄盆具有较高的土壤氧化还原电位,初步说明秋茄比木榄更能忍受水渍,且这两种植物对水渍可能

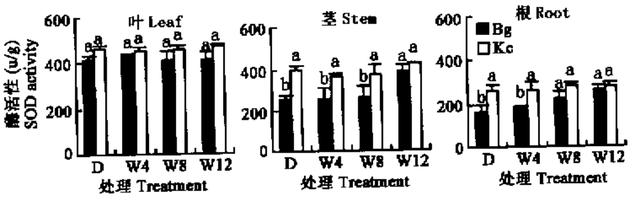

图 7 木榄(Bg)和秋茄(Kc)叶、茎、根超氧化物歧化酶活性对水渍的反应

Fig. 7 Responses of superoxide dismutase (SOD) activity in leaf, stem and root of *B. gymnorrhiza* (Bg) and *K. candel* (Kc) to waterlogging

存在某些生长和生理特点上的差异。

木榄和秋茄对水渍不同的生长反应也表明这两种红树植物存在不同的耐水渍能力。木榄的相对生长率随淹水处理时间的增加而减小,但排水处理与淹水处理间秋茄的相对生长率无显著差异(图 2)。这说明木榄比秋茄对水渍更敏感。野外观察也表明秋茄比木榄更耐水淹,因为秋茄生长的潮位较低,受潮水淹浸的时间更长[8]。

秋茄具有较小的 S/R 值,即更多的生物量分配到根部,这也说明其更能耐水淹。Pezeshki 研究得出,亮叶白骨壤比大红树具有较高的 S/R 值,且前者比后者对低氧化还原电位(与水渍类似)更敏感[4],这与本文的结论一致。

3.2 生理反应

前人的研究大多表明,水渍使植物叶绿素含量减少或光合作用减弱[16]。然而,本研究表明水渍并不导致木榄和秋茄光合色素的减少,12 周的淹水处理反而使光合色素含量增加,说明水渍并不导致这两种红树植物光合作用的减弱。

McKee 的研究表明,根区缺氧时对水渍更敏感的亮叶白骨壤和假红树的根系呼吸率比更耐水渍的大红树降低程度更大[17]。本研究中木榄和秋茄排水处理组、淹水 4 周处理组和淹水 8 周处理组间根系活力均无显著差异(图 3),说明两种植物均有一定的耐水渍能力。但在淹水 12 周处理组二者的根系活力对水渍有不同反应,木榄的值有所减小而秋茄的值显著增加。这也说明秋茄比木榄更能长期耐水渍。

Sung 的研究显示,水渍将抑制较不耐水渍的菜豆的叶片硝酸盐还原酶活性[18]。淹水 12 周处理却使木榄和秋茄的叶片硝酸盐还原酶活性均增加(图 5),证明这两种红树植物均较耐水渍,而秋茄则较木榄更耐水渍,因为秋茄的叶片硝酸盐还原酶活性有更大的增加程度。淹水 12 周处理也导致两种植物的茎以及秋茄根硝酸盐还原酶活性的增加。

研究发现水淹时更不耐水渍的植物脂质过氧化程度更高[19]。在缺氧环境(如水渍)中,耐水渍种类超氧化物歧化酶活性增加[20]。超氧化物歧化酶活性的增加有助于植物抵抗淹水逆境所带来的膜脂过氧化的伤害。秋茄比木榄具有更高的过氧化物酶和超氧化物歧化酶活性(图 7),进一步说明秋茄比木榄具有更强的耐水渍能力。

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