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大强度去叶对棉花叶绿素和保护酶系的影响

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摘要：研究了大强度去叶对棉花叶绿素和保护酶系的影响。结果表明，75%去叶和 100%去叶的大强度去叶不会促使棉花产生超补偿现象，而使棉花成铃数分别减少 5.4%和 9.8%。在短期内大强度去叶可使棉花新生叶片增大、叶绿素含量下降。75%去叶和 100%去叶处理还使得棉花叶中蛋白质含量下降，POD 酶活性上升、PPO 酶活性下降，但 POD 酶比活力和 PPO 酶的比活力都上升。说明大强度去叶不仅对植物造成了严重伤害，而且破坏了棉花植株的内稳态平衡。植物不能迅速调整内稳态平衡（homeostasis）恢复元气，最终棉花也不会产生超补偿现象，此时植物处于伤害状态。内稳态变化可能存在信号分子。

关键词：大强度；去叶；超补偿；叶绿素；保护酶

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Activities of chlorophyll and protective enzyme systems in cotton plants *Gossypium hirsutum* L. with heavy leaf removal by no overcompensation

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Abstract: When 8 squares are removed from each cotton plant, simulating bollworm herbivory, the cotton fiber yield in the final harvest will increase by 10% ~ 30%. This kind of phenomenon that small damages are beneficial to plants themselves is called overcompensation, which has become a hot focus in ecology and evolution studies in recent years. Besides cotton, many scientists have also found a lot of other plants that have this characteristic, such as grass, tree and vegetable. The conditions required for producing overcompensation for a plant include developmental stage, sunlight, damage extent, damage sorts, etc. Our previous study has shown that 50% leaf removal from total canopy area, simulating insect herbivory, could increase boll number by 24.4%. Furthermore, the peroxidase (POD) and polyphenol oxidase (PPO) activity were also changeable. This paper succeeds last experimental study of leaf removal, but we emphasized to observe the effect of larger extent of leaf removal on cotton growth and development and on the occurrence of overcompensation. Particularly, this paper studies chlorophyll and protective enzyme systems in cotton plants *Gossypium hirsutum* L. with 75% and 100% leaf removal respectively, which belonged evidently to heavy leaf removal, of the total canopy leaf area at the early stage of primary anthesis. The results show that no overcompensation phenomenon with a higher cotton fiber yield produced in both cases of 75% and 100% leaf removal, whereas these cotton plants having obvious decreases in boll number of 5.4% and 9.8%, respectively. The new-born leaves on treated plants always presented larger area than that of control and the content of chlorophyll in these new-born leaves decreased during a short period. The level in chlorophyll content in leaves of 75% leaf removal and 100% leaf removal were 19.7% and 20.1% lower than that of control one week after leaf removal. In the meantime, the treatments for herbivory simulation of 75% leaf removal and 100% leaf removal decreased protein content in cotton leaves. One week after leaf removal, the protein content in 75% leaf removal was

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7.4% lower than that of control and 100% leaf removal was 23.1% lower than that of control. Importantly, heavy leaf removal made the highest point of protein content on protein curve appear one week later for the cotton plants with treatment of 75% leaf removal and one more week later for the cotton plants with treatment of 100% leaf removal compared with control. The plants with large degree of leaf removal also had an enhanced activity of peroxidase (POD) but a lowered activity of polyphenol oxidase (PPO) in new-born leaves. Two weeks after leaf removal, cotton leaves with 75% leaf removal had a POD activity 18.0% higher than control and 100% leaf removal had a POD activity 18.8% higher than control. Cotton leaves with 75% leaf removal had a PPO activity 7.0% lower than control and 100% leaf removal had a PPO activity 9.3% lower than control one week after leaf removal. But the specific activity of both POD and PPO increased. All these experimental data suggest that heavy leaf removal not only wrecked the cotton plant homeostasis but also brought about cotton plant serious damage. The wrecked plants with small amount of proteins resulted from heavy leaf removal might be less resistant to other insect or non-insect infestations and could not recover easily from the damage so that they could correctly regulate their own metabolic machine going up onto the regular high level. The damaged homeostasis might have outachieved the modulation limit of plant resistance and functional induction of transnormal ability. So, cotton plants with treatment of heavy leaf removal of 75% and 100% leaf removal at the early stage of primary anthesis could only give expressions of damage status. Together with the previous study, we conclude that if we want to get overcompenation on cotton plants from leaf loss, we should strictly confine the extent of leaf loss to no more than 75% leaf removal. In agriculture, we can use this biological effect resulted from overcompensation to make certain methods to increase agricultural yield. Most crops are plants with high level of endurance for environmental stresses. If we positively make proper intensive artificial mechanical wounds as well as metabolic balance tissue loss instead of those irregular insect and animal herbivory or environmental stress, it is possible for us to get a good harvest without further utilization of fertilizer and plant hormones. In the meantime, the overcompensatory effect also implies an elevation upon concrete threshold of pest management, resulting in reducing the amount of insecticides and pesticides used for insect and pest management and saving the time for farmers. Large scale of application of pesticides in pest control often causes directly soil contamination and environmental air pollution, which severely influence our life quality. So tissue balance and small damage research to plants and animals have great importance to ecology. It seems that there could be chemical signals coming from homeostasis change in plants. These signals that might be small molecular substance, possibly in company with HSP protein, could move from damaged leaf tissues to the new-born leaves, after a long distance transport and transducing over petioles and stems, and regulate the activities of POD and PPO in new-born leaves. This signaling mechanism could be at least in part of the mechanism of overcompensation. If so, we will be thankful that ecology ultimately links to molecular biology. This finding may be interesting to some scientists in the field of molecular biology who have demonstrated that the ubiquitous protein chaperone hsp90 regulates more than 100 proteins involved in cellular signalling. But what factor directly enhances the specific activity of PPO like Ca^{2+} iron remains to be elucidated. This should be our next study direction of work.

Key words: heavy degree; leaf removal; overcompensation; chlorophyll; protective enzyme

模拟棉铃虫侵害对棉花每株摘除8个早蕾,可以使棉花纤维最终增产10%～30%[1]。植物具有的这种少许伤害有益的自然现象,在自然界中增加了物种的生存竞争力,而在农业生产中则可以增加农业收成[2]。因此,超补偿现象[3,4]研究引起了人们的重视,成为近年来分子生态学研究的一个热点。在棉花生长的环境中有许多活跃昆虫以棉花叶片作为食物。这些昆群取食不仅使得植物遭受严重的机械损伤,而且也使整株叶面积和光合面积减小,植物固有的内稳态平衡破坏。因此作者认为去叶实验不能简单等同于植物机械损伤(wounding)。对棉花实施去叶处理可以引发超补偿现象,50%叶面积损失最终使棉花增产24.4%[5]。但对于棉花超补偿可以忍耐的最大失叶程度,还没有见到有关报道。本研究加大植物受害程度,分别给予棉株75%和100%的生长初期叶面积去叶处理,进一步研究植物的"少许伤害有益"现象和超补偿作用限度,探讨植物超补偿作用分子生态学。

1 材料和方法

1.1 供试材料和处理设置

实验采用陆地棉(*Gossypium hirsutum* L.)为植物供试材料,品种为中棉所13,种植地点为河北省霸州市。种子经硫酸脱绒,于4月25日露地直播于试验田中。棉苗株行距为0.24m,0.62m。土壤肥力上等,田间常规栽培管理,适时灌溉,严格防治害虫。在现蕾初期即平均每株有8个花蕾时进行去叶实验,时为6月25日,以模拟棉田害虫为害。去叶实验共设2个处理,1个对照。2个处理为:75%去叶,去除单株棉花总叶面积的3/4,去时全部展开叶每个叶片去掉3/4叶面;100%去叶,去除此时单株总叶面积的全部,去时将全部叶片去掉。

设不去叶的正常生长植株为对照(CK)。去叶时的具体方法是用剪刀逐叶进行剪除,75%去叶时先沿棉花叶片中脉剪去每一叶的1/2叶面,不伤中脉。然后将剩余的半片叶用剪刀沿叶脉中部垂直于叶脉再剪除一半,叶脉一半也被剪去,留取一半叶脉于剩余叶面上。剩余叶面是近轴部分右1/4叶面。100%去叶时沿叶面与叶柄相接处用剪刀剪去叶面,留完整叶脉于棉花植株上。剪除时选用的被剪除处理叶片全部为棉株上的完全展开叶,而且由于棉花生长发育进程的缘故,此时的处理叶片全部都是棉花主茎叶片。在整株上叶片剪除顺序为先上后下,先剪棉花植株上部分叶片,后剪基部叶片。在一个叶片上,剪除的叶片部分顺序是由上而下看棉株,自棉花叶近轴端向外看时棉叶的左半部分先被剪除,然后再依次为右半部分叶片。处理及对照各重复3次,每小区面积为20m^2,田间随机排列,共计小区数3×3=9个。然后,随棉花发育的时间进程,现场观察并定期取样带入实验室内进行生理生化分析,取叶样位置为完全展开的倒三叶,它是棉花的功能叶片。由于棉花发育迅速出叶快,故所取样叶都不是那些受伤直接被剪的叶片,而是完整新生叶片。其它分析测定根据需要取相应叶位的叶片。

1.2 棉花发育及保护酶系测定

叶绿素含量测定 取棉花功能叶片0.2g,用80%丙酮研磨提取叶中叶绿素,用UV-754型分光光度计测定其光吸收$O.D_{663}$、$O.D_{645}$、$O.D_{440}$,然后计算叶绿素含量[5,6]。以80%丙酮为空白对照。

棉花叶中蛋白质含量测定 用50 mmol/L pH=7.0的PBS缓冲液冰浴研磨提取棉花功能叶片中的蛋白质含量,5 000g离心10 min,取上清液用紫外法测定蛋白质含量。测定$O.D_{260}$,$O.D_{280}$,查紫外法对照表得R值,F由公式$F=1.55-1/1.32R$计算得出。所得数据为可溶性蛋白质含量。

棉花叶中过氧化物酶(POD)活性测定 取上述测定蛋白质含量时获得的蛋白质上清液作为POD酶粗提液,来测定棉花叶中的过氧化物酶POD活性。反应体系包括2.9 ml 50mmol/L pH=5.91 PBS,1.0 ml 50mmol/L愈创木酚,1.0 ml 2% H_2O_2,0.5ml酶粗提液。反应体系在加入1.0 ml 2% H_2O_2后迅速于470nm波长(UV-754紫外可见分光光度计)下测定体系1min内的O.D值变化,计算酶活力。然后以上面测得的蛋白质含量为基础计算单位蛋白质中的酶比活力[7~9]。

多酚氧化酶(PPO)活性分析。取蛋白质含量测定得到的上清液作为测定棉花叶中多酚氧化酶PPO活性的酶粗提液。PPO活性反应体系包括3.9 ml 50mmol/L pH=5.91 PBS,1.0 ml 0.1 mmol/L邻苯二酚,0.5 ml酶粗提液。反应在室温下反应15 min,于525 nm波长下测定O.D值,计算酶活力。然后,以上面测得的蛋白质含量为基础,计算单位蛋白质中的酶比活力[8,9]。

每项生理指标测定均重复3次,每次2个平行实验。

2 实验结果

2.1 叶绿素含量

棉花在遭受大强度去叶处理后植株并不死亡,而是顽强地努力生出新叶,特别是全部去叶的棉花植株。在剪叶处理的一段时间(6月25日左右),平均每2d就可以长出一个新的完全展开叶片。因此,在1周时,已经有完全展开的3片棉叶,可以满足生理学以及生物化学的分析需要。分析测定棉花功能叶片中叶绿素的含量,结果如图1所示。大强度去叶致使棉花新生叶片中叶绿素含量普遍降低。单从人的肉眼在田间就可以很轻易地看出叶色变浅,呈淡绿色。同时看到新叶叶面积增大的现象。实验室测定结果表明,1周时叶绿素含

量由高到低依次为:CK、75% 去叶、100% 去叶。75%去叶处理比对照低 19.7%,100%去叶处理比对照低 20.1%($p<0.01$)。之后随着发育进程棉花新生叶片逐渐增多,叶片叶绿素含量逐渐增加,叶片颜色也逐渐加深。

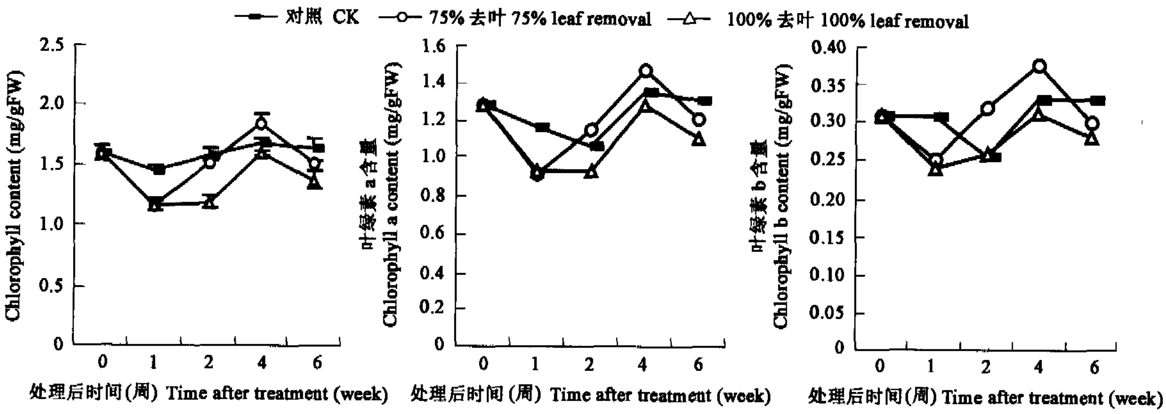

图 1　模拟昆虫取食大强度去叶对棉花新生叶片中叶绿素含量的影响(平均数 ± 标准差,下同)

Fig.1　The effect of heavy leaf removal by simulating insect herbivory on chlorophyll content in the new-born leaves of cotton (means ± SD, the same below)

2.2　蛋白质含量变化

叶中蛋白质含量随时间而呈现出先升高再降低的抛物线式变化趋势(图 2),最高点在 7 月 2 日(处理后 1 周)。7 月 2 日是棉花始花期(anthesis),此时棉花体内各项代谢最为旺盛,需要较多的各项代谢酶系,因而叶中蛋白质含量较高。去叶处理能改变叶片中蛋白质含量随生长进程的变化趋势,使得 75%去叶的蛋白质含量最高点推迟 1 周,100%去叶处理更向后。至 2 周时 3 者的蛋白质含量趋向接近,75%去叶高于对照。在所进行的 5 次测定中,多数情况下处理植株叶片中的蛋白质含量都低于对照。

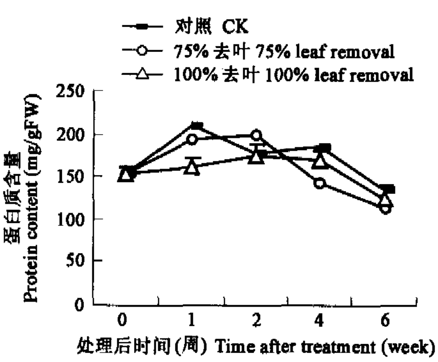

图 2　模拟昆虫取食大强度去叶对棉花叶中蛋白质含量的影响

Fig.2　The effect of heavy defoliation by simulating insect herbivory on protein content in the new-born leaves of cotton

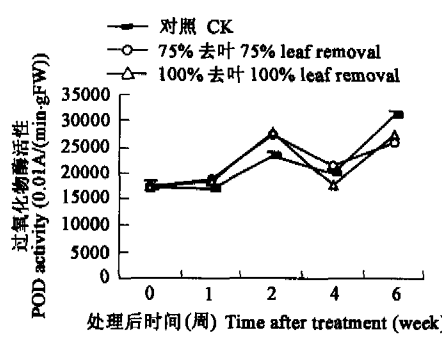

图 3　大强度去叶对棉花叶中过氧化物酶活性的影响

Fig.3　The effect of heavy leaf removal on peroxidase (POD) activity in the new-born leaves of cotton

2.3　过氧化物酶活性 (POD)

大强度去叶处理可以增加棉花叶片中的 POD 酶活性。2 周时 75%去叶比对照增高 18.0%, 100%去叶比对照增加 18.8%($p<0.01$)。这与棉花丢失叶面积后棉花体内的代谢调整和过氧化物的清除相关联 (图 3)。4 周时过氧化物酶活性发生变化,到 6 周时两个处理都低于对照,75%去叶比对照低 16.5%,100%去叶处理比对照低 11.3%($p<0.01$),75%处理稍微低于 100%处理。

2.4　多酚氧化酶 PPO 活性变化

多酚氧化酶的实验结果表明,随着棉花的发育进程深入,棉花叶中多酚氧化酶活性持续走高。这与棉花

发育趋向衰老相关联。去叶处理在短期内可以降低棉花叶中的PPO酶活性,1周时75%去叶处理PPO活性比对照低7.0%,100%去叶处理比对照低9.3%(图4)($p<0.05$)。至2周时75%去叶处理和100%去叶处理的PPO活性都高于对照($p<0.01$)。并且100%去叶处理的活性一直到最后PPO活性都高于对照。去叶处理后4周,100%去叶的PPO酶活性略高于对照,而75%去叶的PPO活性略低于对照。

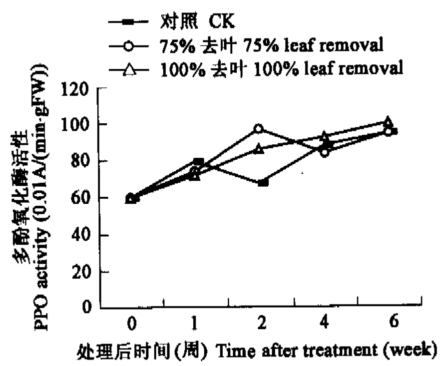

图4 大强度去叶后棉花叶中的多酚氧化酶活性

Fig.4 The effect of heavy leaf removal on the activity of polyphenol oxidase (PPO) in the new-born leaves of cotton

2.5 POD、PPO酶比活力的变化趋势

分析棉花叶中POD和PPO两种酶的比活力,发现无论是POD还是PPO,它们的比活力都随棉花发育而明显逐渐增加,这也说明植株衰老进程中POD、PPO增强,即单位蛋白质中的酶量增加(图5)。处理后1周,POD比活力随着去叶程度加深而顺序增加。至第6周时,各处理间以及与对照间的比活力已基本相同。PPO比活力至2周时,75%去叶和100%去叶两者的PPO比活力基本相同,都高于对照。而至第4周仍然是处理株高于对照,顺序是75%去叶 > 100%去叶 > CK($p<0.05$);这种趋势一直维持到第6周(75%与CK之间 $p<0.01$,100%与CK之间 $p<0.05$)。

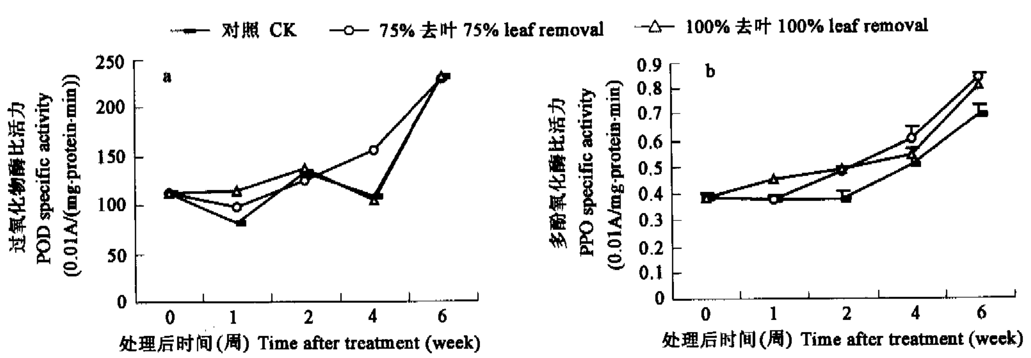

图5 大强度去叶后棉花新生叶中过氧化物酶比活力(a)、多酚氧化酶比活力(b)

Fig.5 The effect of heavy defoliation on the specific activity of peroxidase (POD) (a) and polyphenol oxidase (PPO) (b) in the new-born leaves of cotton

3 讨论

适度的外因导致叶片和花蕾损失最终会导致棉花发生超补偿现象。去蕾实验的超补偿已经定论[1],去叶情形见文献[5]的50%去叶实验中得到了充分的体现,50%去叶可使得棉花成铃数增加24.4%。而大强度去叶则使得棉花减产,本实验中75%去叶和100%去叶处理分别使棉花最终成铃数减少5.4%和9.8%。因此,超补偿的产生具有严格的实验条件。离开这些条件,将不能使得植物产生超补偿[6]。

大强度去叶可使棉花株高受到显著影响的同时[5],棉花新生叶片表现出与众不同。100%去叶可使得棉花叶片叶绿素含量大幅度降低、并使得新出叶片叶面积加大。这种现象可以使得棉花在缺乏营养来源的条件下,迅速地获得最多的光合作用产物。可能是植物应激反应的一种。迅速扩大的棉花叶片冲淡了棉花叶片中的营养物质和细胞结构物质,这其中也包括叶绿体以及其中的叶绿素。然而这些影响经过一段时间后已经基本上消失,叶绿素和光合作用基本恢复正常,并发生叶绿素含量超补偿现象(75%去叶,4周)。在叶片中,叶绿素含量降低的情况下叶片叶面积升高,这在文献中还是第一次报道。这种叶绿素含量的调整和叶片发育的改变调整是单纯机械损伤理论[7~9]不能解释的。

去叶处理能改变叶片中蛋白质含量随生长进程的变化趋势,使75%去叶处理叶中蛋白质含量最高点比对照推迟1周,而使得100%去叶处理叶中蛋白质含量最高点比75%更加推迟。多数情况下,大强度去叶使

得棉花叶中的蛋白质含量下降。这不同于轻度去叶 25%、50% 去叶常常增加棉花叶中蛋白质含量的情形[5,10]。曾有报道,植物在遭受逆境时包括高温、低温、干旱、病虫侵袭时可以合成特异蛋白质,称谓热击蛋白(hsp)[11]。曾在花生上得出结论,花生在受到干旱胁迫时蛋白质含量即快速增加,然后蛋白质含量下降[12]。蛋白质是生物生命活动的最基本物质,也是叶片中光合作用关键酶 RuBP 羧化酶的主要内容。因此,在棉花遭受严重机械损伤并内稳态平衡(homeostasis)遭受严重破坏时,植物光合面积减小,植物蛋白质代谢受到影响,蛋白质合成受阻。这样就减低了植物叶片的生命代谢水平,使得棉花抗逆性水平下降。曾有研究报道,在玉米上去叶可以降低其对青枯病病害的抵抗力,而去花则增加抗病性,这与本实验的研究结果具有相同之处[13]。光合功能衰退过程中一个最明显的指标是叶绿素和蛋白质含量的下降。也是植物在遭受内稳态平衡破坏后不能迅速恢复元气的具体体现。

作为生物学保护酶系的过氧化物酶和多酚氧化酶具有保护植物不受过氧化、高温等逆境因子常常造成的后果的影响[14,15],以便维持植物正常的新陈代谢。大强度去叶处理可以增加棉花叶片中的 POD 酶活性。2 周时 75%去叶比对照增高 18.0%, 100%去叶比对照增加 18.8%。这与棉花丢失叶面积后棉花体内的代谢调整和过氧化物的清除相关联。这与从轻度去叶上获得的结果类似[5]。但在多酚氧化酶上,去叶处理在短期内可以降低棉花叶中的 PPO 酶活性,1 周时 75%去叶处理 PPO 活性比对照低 7.0%,100%去叶处理比对照低 9.3%。而之后 PPO 酶活性随着去叶程度的加大而渐次表现增强。这暗示由于去叶程度过大早期已对植物造成了危害;而随着棉花的复原逐步进行,后来棉花合成了较多的 PPO。说明 POD 和 PPO 的作用可能不同。而且许多文献报道,POD 和 PPO 的酶活性在植物中的作用不尽相同[16,17]。对比活力的测定结果也说明 POD 和 PPO 在两个处理中的不同。处理后 1 周,75%去叶处理和 100%去叶处理植株棉花叶片中的 POD 比活力随着去叶程度加深而顺序增加。至第 6 周时,各处理间以及与对照间的比活力已基本相同。这可能与 POD 激活或 POD 合成增加有关。PPO 比活力在多数情况下高于对照,与 POD 比活力形成了鲜明的对比。这暗示着单位蛋白质中的 PPO 活性增强。可能是因为某些因子激活了 PPO 开始上升。这些情形不同于具有超补偿功能的 50%去叶情形[5]。因此,大强度去叶可能刺激破坏了与棉花的某些内稳态相关的代谢过程,导致能量消耗过大,用来清除过氧化物的 PPO 不能被及时合成,而只能以增加比活力来改变清除棉花具有的伤害因素,所以造成 PPO 含量下降。这种情况说明 PPO 稍微不同于 POD。本研究中测定使用的叶片都是新生完整叶片,所有结果似乎表明有某种内稳态失衡信号分子从受伤叶片发出调节着新生叶片中的 POD 和 PPO,而该信号因子对二者作用的强度和结果却不尽相同。该信号因子的形态可以跨过叶柄、叶基,穿过棉花茎并再次跨过叶基、叶柄而到达新生叶片。单一 hsp 蛋白质本身作为这种长距离信号分子[11]似乎不太现实,必须有其他小分子信号物质的参与[18,19]。

本文的一个重要结论是,超过 75%去叶就不能产生超补偿。因此,在实际的生产实践中利用植物自身的诱导能力来实现增产目的时应当注意这一点。同时,在大强度去叶情形下,有某种因子刺激了 PPO 的活性增强,但 PPO 总活性下降。这些激活因子可能是 Ca^{2+},也可能是其他离子,而对于总活性下降的原因,尚需作进一步研究。

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