剪叶损伤与昆虫取食对兴安落叶松(*Larix gmelinii*)针叶中缩合单宁诱导作用的差异

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摘要:单宁是植物内与抗虫性相关的重要次生代谢物质。为了研究昆虫取食及剪叶诱导对兴安落叶松(*Larix gmelinii*)针叶内缩合单宁含量的影响,用剪叶法和落叶松毛虫(*Dendrolimus superans*)幼虫取食处理 5 年生兴安落叶松苗,以香草醛-盐酸法测定其剩余健康针叶内缩合单宁含量的变化。结果表明:(1)处理后 1 ~ 10d,剪叶 4 枝 75% ,8 枝 50% 、75% ,12 枝 25% 、50% 、75% 及虫伤 4 枝 75% 的兴安落叶松健康针叶内的缩合单宁含量均明显高于对照($P<0.01$),15d 时,剪叶 8 枝 75% ,12 枝 50% 的兴安落叶松针叶内的缩合单宁含量仍高于对照($P<0.05$),说明剪叶与虫伤处理均能诱导缩合单宁含量增加。(2)剪叶 4 枝 75% ,8 枝 50% ,12 枝 25% 、75% 的处理之间,诱导的缩合单宁含量差异不显著($P>0.05$)。剪叶 8 枝 75% ,12 枝 50% 诱导缩合单宁含量增加幅度比其它剪叶处理大,且诱导持续时间长。说明剪叶程度虽能影响缩合单宁含量,但二者并不呈线性关系。(3)剪叶 4 枝 75% 在 5d 时诱导缩合单宁含量最高,虫伤 4 枝 75% 在 10d 时诱导缩合单宁含量最高,说明剪叶诱导的缩合单宁含量高峰早于虫伤处理。但处理后 1 ~ 10d,剪叶及虫伤 4 枝 75% 的落叶松针叶内缩合单宁含量均明显高于对照($P<0.01$ 或 $P<0.05$),之后与对照差异不显著($P>0.05$),说明在受到诱导处理后,兴安落叶松产生应激反应,使其针叶内缩合单宁含量在一定时间内先增加,后逐渐恢复到正常水平。由上可见,可以采取适当的损伤处理取得与昆虫取食相似的兴安落叶松抗性反应。

关键词:兴安落叶松;缩合单宁;剪叶损伤;昆虫取食

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Content differences of condensed tannin in needles of *Larix gmelinii* by cutting needles and insect feeding

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Abstract: The influences of insect feeding and cutting needles to condensed tannin contents in needles of *Larix gmelinii* were studied. The needles of five-year old *L. gmelinii* were treated with cutting needles and larva feeding of *Dendrolimus superans*, and the changes of condensed tannin contents in needles on the untreated branches were detected by vanillin-HCL assay. The results showed that: (1) day 1 to day 10 after treated, the condensed tannin contents in undamaged needles of seven treatments (75% needles on four branches, 50% or 75% of needles on eight branches, and 25% or 50% or 75% needles on twelve branches were cut off and 75% needles on four branches were fed), were significantly higher than that in control ($P<0.01$). By day 15, the condensed tannin contents in undamaged needles of two treatments (75% needles on eight branches and 50% needles on twelve branches were cut) were still higher significantly than that in control ($P<0.05$). These results suggested that both cutting needles and insect feeding could induce the increase of condensed tannin contents. (2) There were no significant differences of condensed tannin contents between four treatments (cutting off 75%

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needles on four or twelve branches, 50% needles on eight branches and 25% needles on twelve branches) ($P > 0.05$). Whereas, the changes of condensed tannin contents after cutting out 75% needles on eight branches and 50% needles on twelve branches were much higher than other cutting treatments, and the remained time of the changes was also longer. These implied that degrees of cutting needles could influence condensed tannin contents, but there were no linear relationships between them. (3) A peak of condensed tannin contents in the needles of treatment induced by cutting off 75% needles of each four branches appeared on day 5, while on day 10 for those induced by eating up 75% needles on four branches, indicating that the peak of condensed tannin contents induced by cutting needles appears earlier than that induced by insect feeding. But the condensed tannin contents in undamaged needles induced by either cutting off or eating up 75% needles of each four branches were higher than control within 10 days after treated from first day to 10th day ($P < 0.01$ or $P < 0.05$), and then the differences were not significant ($P > 0.05$), which indicated that a stress response was produced with the increase of condensed tannin contents in needles within certain time when *L. gmelinii* was induced, and then came back to the natural level gradually. The results suggest that appropriate wound-treatments, which can simulate the insect's feeding, can be used to induce *L. gmelinii* defense responses.

Key Words: *Larix gmelinii*; condensed tannin; cutting needles; insect feeding

诱导系统抗性(induced systemic resistance, ISR)可作为增强植物防御能力的生物调控机制[1]。植物体受到机械损伤或昆虫取食后,在伤口部位产生大量的防御化合物,使植物本身对害虫产生抗性,形成化学防御体系[2,3]。植物次生代谢物(plant secondary metabolites)是植物化学防御体系的主要基础。植物单宁(vegetable tannin)是植物中以诱导型和组成型方式存在的次生物质,是一类具有多抗性的酚类物质[4],能与蛋白质发生特异性结合影响昆虫的取食、消化、生长发育等,是其对植物具有防御作用的关键[5]。植物单宁主要以高浓度、高剂量方式防御昆虫取食和危害,属于"数量防御"型次生物质[6],植物体内的单宁含量会因植株受害而升高,其含量可作为树种的抗性指标[7,8]。近来已有学者提出把单宁含量作为松树受害程度的一个检测因子[9]。已有研究证明,昆虫取食或机械损伤均可诱导马尾松针叶内叶单宁含量升高[10]。兴安落叶松(*Larix gmelinii*)是东北地区主要树种,其叶部重要害虫——落叶松毛虫(*Dendrolimus superans* (Butler))近年在黑龙江、吉林和内蒙古林区频繁发生,它不仅危害成林而且危害苗木,给林业造成严重经济损失。本试验采用模拟虫害剪叶及昆虫取食处理兴安落叶松,研究不同损伤程度、不同昆虫取食程度对兴安落叶松针叶内缩合单宁含量诱导的差异性。

1 材料与方法

1.1 试验材料

植物材料为在东北林业大学帽儿山林场老山实验站网棚内培育的5年生兴安落叶松苗。选取长势均衡的健康苗为试验用苗;将采自内蒙古克什克腾旗的落叶松毛虫蛹,室内羽化,交配产卵,饲养孵化幼虫至3龄作为试验虫源。

1.2 试验方法

1.2.1 针叶处理与采集

幼虫取食处理 将选定苗木分成3组做取食4枝处理,在树冠东、南、西、北4个方向各选1侧枝,在其侧枝的当年生枝的叶部接上3龄落叶松毛虫幼虫,用纱网罩住接虫枝条。3组的各侧枝接虫量分别为10头、20头、30头,两天内使各侧枝针叶受害程度分别达到25%、50%、75%。待达到要求的受害程度时,取下幼虫,开始计时。

剪叶处理 将选定苗木做剪叶4枝、8枝、12枝3种处理方式,分别在所选苗木树冠的东、南、西、北4个方向各选1、2、3个侧枝,对所选各侧枝当年生枝上的针叶进行剪叶处理,每种处理设3个剪叶程度,分别剪去每枝条针叶的25%、50%、75%。对照样苗不做任何处理。

分别在取下虫子和剪叶后的第 1、5、10、15、20 天,分别在每株处理苗上均匀摘取不同部位的剩余未损伤的针叶,并将在同一株上所采的针叶相互混合,装入夹链袋中,迅速放入冰盒内以保持其活力,带回室内,于 -20℃条件下保存于冰箱中,备用。

以上每种处理及对照均设 3 个重复,每个重复均处理 3 株样树。

1.2.2 缩合单宁提取与测定(参照文献[11]略做改动)

用德国 D-37520 Osterode 型冷冻干燥机将针叶鲜样于 -57℃条件下,冷冻干燥 24 h,之后迅速冰浴研磨至粉末状,过 60 目筛后,置于 -20℃条件下密封保存备用。精确称取样品冻干粉 50 mg,放入具塞试管中,加入 70% 的甲醇 5 ml,封口摇匀,在室温下放置 24 h,于 4℃条件下 5000 r/min 离心 10 min,取上清液作为待测提取液。

用 4 g 香草醛溶于 100 ml 纯甲醇中,配制 4% 的香草醛甲醇溶液,用前新配制。分别取 4% 的香草醛甲醇溶液 3 ml、浓盐酸 1.5 ml 和待测提取液 0.5 ml 加入以铝箔遮光的具塞试管中摇匀,于 20℃条件下水浴 20 min。以 4% 的香草醛甲醇溶液 3 ml、浓盐酸 1.5 ml 和 70% 的甲醇 0.5 ml 作空白对照,用 752 型分光光度计在 510 nm 下比色,重复 3 次,记录吸光值。以儿茶素(SIGMA 公司)为标准样品[11]绘制标准曲线,根据其标准曲线计算出提取液缩合单宁含量。

儿茶素标准曲线的绘制:取 1.0 g/L 儿茶素溶液配制梯度浓度标准溶液,分别在 510 nm 处测定吸光值(同上),以儿茶素浓度为横坐标,吸光值为纵坐标绘制标准曲线。测定的标准曲线方程为:$Y = 1.3189X + 0.0259$, $R^2 = 0.9991$,其中 Y 是吸光值,X 是浓度($mg \cdot mL^{-1}$)。线性范围为:0 ~ 0.7 $mg \cdot mL^{-1}$。

2 数据的统计与分析

用 SPSS 11.5 软件进行统计分析,计算缩合单宁含量的平均值和标准差后,以 One-Way ANOVA 分析,以 LSD($\alpha = 0.05$ 或 $\alpha = 0.01$)分别检验在 1、5、10、15、20d 时,不同程度剪叶和昆虫取食处理后,兴安落叶松针叶内缩合单宁含量与对照间的差异显著性,并对剪叶处理程度相同而方式不同的兴安落叶松针叶内缩合单宁含量以及处理 4 枝 25%、50%、75% 的剪叶及昆虫取食诱导的缩合单宁含量进行分析比较。

3 结果与分析

3.1 剪叶对兴安落叶松针叶内缩合单宁含量的影响

3.1.1 剪叶程度及方式不同的兴安落叶松针叶内缩合单宁含量的变化

与对照相比,剪叶 4 枝、8 枝、12 枝的处理均能诱导缩合单宁含量变化(图 1)。与对照相比,处理后 1 ~ 10d,剪叶 4 枝 75%,8 枝 50%、75%,12 枝 25%、50%、75% 的兴安落叶松针叶内缩合单宁含量均明显高于对照($P < 0.01$),5d 时诱导缩合单宁含量均达到高峰,分别为对照的 125%、131.5%、153.6%、128.4%、145.4%、129%。之后诱导的缩合单宁含量有所减少,10d 之后,缩合单宁含量逐渐趋于对照水平。15d 时,仅剪叶 8 枝 75%,12 枝 50% 的兴安落叶松针叶内缩合单宁含量仍高于对照水平($P_{8枝75\%} = 0.011$, $P_{12枝50\%} = 0.006$),其它剪叶处理的缩合单宁含量均已恢复到对照水平。剪叶 8 枝 75%,12 枝 50% 不仅诱导缩合单宁含量增加幅度比其它剪叶处理大,而且诱导时间长。说明剪叶处理能迅速系统诱导兴安落叶松针叶内缩合单宁的积累,使其含量明显升高,且缩合单宁含量的变化与剪叶程度有关。

3.1.2 剪叶处理程度相同方式不同的兴安落叶松针叶内缩合单宁含量变化

剪叶 4 枝 50% 与剪叶 8 枝 25%(图 2 A)、剪叶 4 枝 75% 与剪叶 12 枝 25%(图 2 B)、剪叶 8 枝 75% 与剪叶 12 枝 50%(图 2 C),是剪叶程度分别相同,而剪叶方式不同的 3 组处理。从图 3 可看出,剪叶程度相同而方式不同的处理对缩合单宁含量的影响差异不显著($P > 0.05$)。说明在剪叶程度一定时,剪叶不同枝数的处理方式对缩合单宁含量影响不大。剪叶程度是诱导缩合单宁变化的关键。

3.2 昆虫取食与剪叶对兴安落叶松针叶内缩合单宁含量影响的比较

方差分析结果表明,处理程度为 4 枝 25% 和 4 枝 50% 时,对照、剪叶及昆虫取食处理针叶中缩合单宁含量均无明显差异($P > 0.05$)。处理程度为4枝75%时,与对照相比,剪叶及昆虫取食处理针叶中缩合单宁

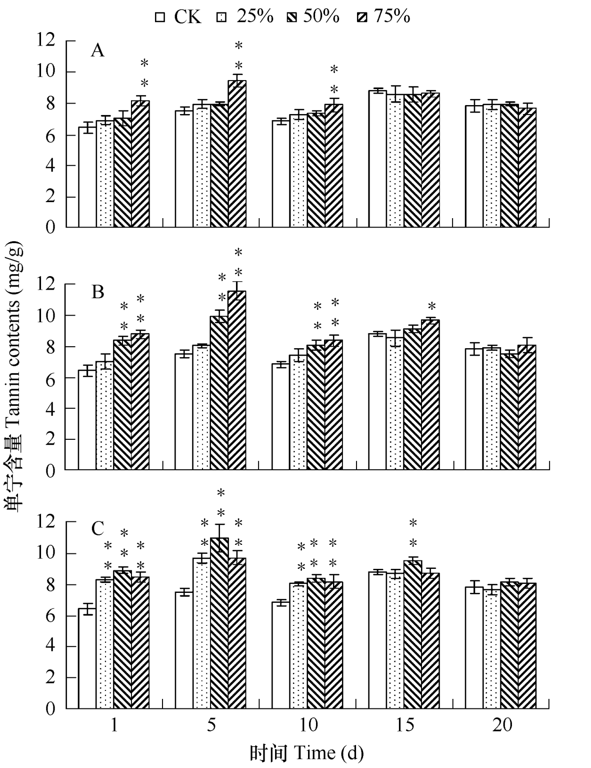

图 1 不同程度剪叶处理后兴安落叶松针叶内缩合单宁含量的变化

Fig. 1 Changes of condensed tannin contents in needles from *Larix gmelinii* after cutting needles of different degrees

A:剪叶 4 枝 Needles being cut from four branches; B:剪叶 8 枝 Needles being cut from eight branches; C:剪叶 12 枝 Needles being cut from twelve branches

数据为平均值 ± 标准差($n=3$),“ * * ”表示与对照差异极显著($P<0.01$),“ * ”表示与对照差异显著($P<0.05$),下同

Data are Mean ± SD ($n=3$), “ * * ” mean significant difference at 0.01 level, “ * ” mean significant difference at 0.05 level, compare with the control, the same below

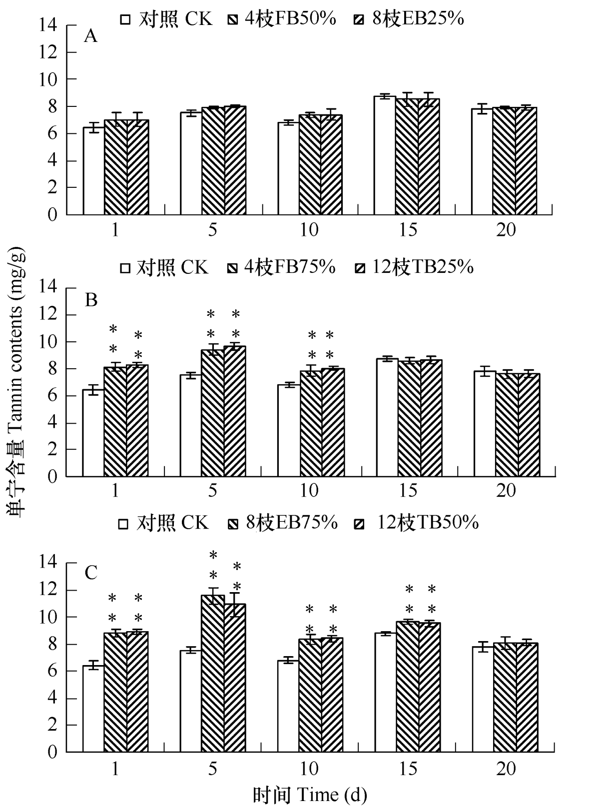

图 2 剪叶处理程度相同方式不同的兴安落叶松针叶内单宁含量变化

Fig. 2 Changes of condensed tannin contents in needles of *Larix gmelinii* after cutting needles of same degree and different modes

FB: four branches; EB: eight branches; TB: twelve branches

A,B,C:分别表示剪叶程度相同而剪叶方式不同的处理 A, B, C: cutting needles of same degree with different modes in each treatment

含量均有明显差异($P<0.01$),二者的缩合单宁含量变化趋势一致。10d 后诱导的量逐渐减少,至第 15 天时,含量恢复到对照水平(图 3)。剪叶处理在 1d、5d 时诱导的缩合单宁含量分别比昆虫取食诱导的缩合单宁含量高 6.11%、7.67%(图 3),在第 10 天时,虫伤处理诱导的缩合单宁含量比剪叶处理高 23.94%(图 3)。说明剪叶能模拟昆虫取食诱导缩合单宁含量增加,且剪叶诱导更迅速。

4 讨论

植物受人为机械损伤或昆虫取食后,伤口部位的果胶质、昆虫口腔分泌物中的活性因子等使植物在损伤部位产生特定原初信号分子[12],激活伤口周围组织的 pin 基因,首先在伤口部位引起植物体局部生理生化反应,启动局部防御系统[13]。与此同时,因损伤诱导产生的内源系统肽运输到整个植株,通过茉莉酸信号途径激活远离伤口组织的 pin 基因,启动系统防御系统[14,15],形成系统获得性抗性(systemic acquired resistance,简称 SAR)[16],从而引起非损伤部位化学物质的变化使植物在短时间内产生最大的防御反应,构建起植物体的防御体系[17]。植物遭受机械损伤后,单宁(分子量为 500 ~ 3000)含量的增加是非挥发性次生物质的一个显著变化[18]。在对兴安落叶松的局部损伤诱导试验中,经 4 枝 75%、8 枝 50%、75%,12 枝 25%、50%、75% 的

剪叶处理后,非损伤针叶内缩合单宁含量均有所增加,说明此程度的剪叶处理对植物的诱导刺激超出了警戒状态的阈值,植物对生长与防御资源做了重新分配。植物单宁的损伤诱导对植物体来说是一种经济有效的防御方式,植物为避免在非胁迫条件下消耗太多资源而影响自身生长,其诱导防御与生长存在动态平衡[9]。因此,剪叶与虫伤处理虽均能迅速诱导缩合单宁含量的增加,但不能一直保持其高含量来抵御侵害,随时间推移缩合单宁含量逐渐恢复到正常水平[19]。

剪叶 8 枝 75% 与剪叶 12 枝 50% 诱导的单宁含量最多,说明此剪叶程度对植物的诱导刺激比较适度。植物的诱导抗性呈"开-关(on-off)"式效应,在一定受害范围内抗性相似[20],所以剪叶 12 枝 75% 诱导缩合单宁含量并不比剪叶 8 枝 75%、12 枝 50% 的多,而且与剪叶 4 枝 75%、8 枝 50%、12 枝 25% 诱导含量相当。因此兴安落叶松针叶内缩合单宁含量的变化幅度虽与剪叶程度的强弱有关,但二者不呈线性关系。

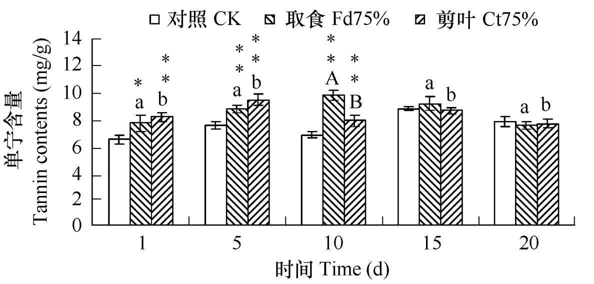

图 3　昆虫取食和剪叶 4 枝 75% 的兴安落叶松针叶内缩合单宁含量变化

Fig. 3　Changes of condensed tannin contents in needles from *Larix gmelinii* after 75% needles on four branches were cut off or fed

Fd: Feeding, Ct: Cutting

不同字母表示剪叶与昆虫取食差异显著(小写字母表示 $P<0.05$,大写字母表示 $P<0.01$)　Different Letters mean significant difference between cutting and feeding(small letter showed $P<0.05$, capital letter showed $P<0.01$)

剪叶造成的机械损伤在作用时间上与昆虫取食造成的机械损伤不同。昆虫取食需要一定时间,对植物危害是逐渐过程;剪叶模拟了昆虫对植物的危害程度而忽视取食过程,作用时间短。本研究结果显示剪叶诱导的缩合单宁含量高峰出现早于虫伤处理,说明剪叶损伤可以更快速地诱导植物产生抗性反应。据研究报道,昆虫取食对植物的影响包括取食造成的机械损伤和口腔分泌物的化学刺激[21],昆虫口腔分泌物在调节植物虫害响应基因的表达中起决定性作用[22~24]。但本研究结果显示,剪叶与昆虫取食两种处理诱导的缩合单宁含量变化的总趋势一致。戈峰等发现人工剪叶模拟危害与害虫危害马尾松类似,同样对松毛虫种群具有调控作用[25]。说明植物对诱导因子的反应有种类差异,对于兴安落叶松而言,剪叶能够取代昆虫取食适时诱导植物产生抗性。对兴安落叶松诱导抗性系统深入的研究,将为开展落叶松毛虫等害虫的生态调控、延长其爆发周期提供新途径,为落叶松诱导抗性的选育和利用提供一个更科学、更客观的思维框架。

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