第 26 卷第 11 期
2006 年 11 月

生　态　学　报
ACTA ECOLOGICA SINICA

Vol. 26 ,No. 11
Nov. ,2006

大气臭氧浓度升高对植物及其昆虫的影响

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摘要 :臭氧是最具危害性的空气污染物之一 ,从 19 世纪中叶开始 ,对流层中的臭氧水平增加了 35 % ,在今后 50～100 年内还将继续升高。臭氧浓度升高对植物生理基本功能、植物体内信号分子以及挥发物都具有不同程度的影响 ,并严重影响作物的产量。臭氧也通过改变植物的原生代谢和次生代谢发生数量而影响植食性昆虫的取食偏嗜性、行为、生长和发育 , 进而影响天敌昆虫的适合度。臭氧还通过改变化学信息物质而影响昆虫的行为。根据国内外研究进展 , 介绍了大气臭氧浓度升高对植物、昆虫的影响 ,并讨论了目前存在的问题和研究前景。

关键词 :臭氧浓度升高 ;植物 ;昆虫 ;影响
文章编号 :1000-0933(2006) 11-3878-07　**中图分类号** :Q142　**文献标识码** :A

The effect of elevated ozone concentration on plants and insects

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Abstract :Ozone is one of the most harmful air pollutants. The concentration of atmospheric ozone has increased since the middle of 19th century and will continue to rise for at least the next 50 − 100 years. Elevated ozone concentration affects plant physiology, signalling among plant cells, and production of plant volatiles to different degrees, and threatens crop yields. The preference, behaviour, growth, and development of insect herbivores are impacted due to the changes in plant primary and secondary metabolism brought about by elevated ozone concentration. Elevated ozone concentration influences insect behaviours by changing semiochemicals. Consequently interactions between herbivores and the next trophic levels are greatly affected. The effect of elevated ozone concentration on plants and insects is summarized based on domestic and foreign research reports. Methological problems associated with research in this area are discussed and our own perspective on future research is provided.

Key words :elevated ozone concentration ; plants ; insects ; effect

臭氧是最具危害性的空气污染。从 19 世纪中叶开始 ,对流层中的臭氧水平增加了 35 %[1] 。美国大气臭氧浓度平均每年升高 1 % ,在未来 40a 里还会升高 3 倍[2] 。今后 20a 中国臭氧前体的释放会成倍增加 ,光氧化剂也会大量增加 ,因此臭氧浓度也会随之增大[3] 。臭氧浓度升高会导致植物光合作用降低 ,从而引起植物营养成分和次生代谢物质的变化 ,以植物为食的植食性昆虫必然会受到不同程度的影响[4] ,进而影响更高营养阶层的寄生性和捕食性昆虫[5～7] 。由于植物和昆虫种类繁多 ,大气臭氧浓度的升高对不同植物上生长的不同昆虫的影响可能是正面的、负面的 ,或者没有影响 ,这取决于植物-植食性昆虫系统的生物特性[8～12] 。国际上非常重视大气臭氧浓度升高对植物和昆虫影响的研究 ,我国这方面的研究刚刚起步。本文将根据国内外研究进展 , 介绍大气臭氧浓度升高对植物和昆虫的影响 ,并对目前存在的问题和研究前景进行讨论。

基金项目 :国家自然科学基金资助项目(30571255)
收稿日期 :2006-03-22 ;**修订日期** :2006-09-29
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致谢 :承芬兰 Kuopio 大学 Jarmo Holopainen 教授惠赠部分文献 ,谨致衷心的感谢。
Foundation item :The project was financially supported by National Natural Science Foundation of China (No. 30571255)
Received date :2006-03-22 ; **Accepted date** :2006-09-29
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1　大气臭氧浓度升高对植物的影响

1.1　臭氧对植物生理基本功能的影响

臭氧是一种强氧化剂,在臭氧的作用下,植物细胞的膜系统、植物的光合作用、呼吸作用以及其他一些生理功能,均会受到一系列的影响[13]。Krupa 和 Jäger 总结了污染空气中的臭氧对植物功能的影响(表 1)[14]。

表 1　臭氧对植物的影响[14]

Table 1　Effects of elevated O_3 concentrations on plants[14]

植物特征 Plant characteristic	对植物的影响 Effect on plants
光合作用 Photosynthesis	大部分物种降低 Decreased in most species
叶片的导电系数 Leaf conductance	敏感物种和品系降低 Decreased in sensitive species and cultivars
水的利用率 Water-use efficiency	敏感物种降低 Decreased in sensitive species
叶面积 Leaf area	敏感物种降低 Decreased in sensitive species
叶片比重 Specific leaf weight	敏感物种增加 Increased in sensitive species
作物成熟率 Crop maturation rate	降低 Decreased
开花 Flowering	花产量、座果、果实产量降低,座果推迟 Decreased floral yield, fruit set and yield, delayed fruit set
干物质产量 Dry matter production and yield	大部分物种降低 Decreased in most species
(物种内)品系的敏感性 Sensitivity between cultivars (within species)	通常变化很大 Frequently large variability
对干旱的敏感性 Drought stress sensitivity	对干旱敏感 Plants become sensitive to drought

植物本身就一直处于原生代谢与次生代谢的交替开放变化过程中,植物体内无论营养物质还是次生物质都处于不断波动的变化中。臭氧能够诱导植物的这一生理过程发生数量或质量的变化。

臭氧对植物原生代谢的影响是引起叶片中含碳化合物和氮素浓度的变化[15,16]。高浓度臭氧导致一些植物叶片氮素大幅度下降[16]:高浓度臭氧会降低颤杨 *Populus tremuloides* 的氮素水平,但淀粉浓度增加[12,17,18];臭氧处理后 7d,番茄 *Lycopersicon esculentum* 叶片中的总氮降低[8]。一些植物对臭氧的反应则是氮素提高:与过滤空气处理相比,用臭氧浓度增加的空气处理欧洲榉,其韧皮部分泌液中氨基酸/糖比值显著提高;臭氧处理的烟草植株氮含量较高[19]。短时间高浓度臭氧处理会增加樟子松 *Pinus sylvestris* 和欧洲云杉 *Picea abies* 幼苗中自由氨基酸浓度[20]。一些植物经过臭氧处理后,氮素含量不变,碳素含量增加:经臭氧处理叙利亚马利筋 *Asclepias syriaca* 的糖分会增加,氨基酸含量不受影响[21];低浓度的臭氧处理不影响樟子松 *Pinus sylvestris* 针叶中的全部游离态氨基酸的浓度,但淀粉的浓度增加[22]。部分植物对臭氧的反应是氮素和碳素含量都降低:臭氧处理通常会降低马利筋 *Asclepias curassavica* 的糖分和蛋白质含量[21]。臭氧对一些植物不发生影响,其氮素和碳素含量都没有变化:与过滤空气处理相比,用臭氧浓度增加的空气处理四季豆,其韧皮部分泌液中氨基酸或糖含量没有显著差异[23]。

对于次生代谢,富集的臭氧降低了颤杨中酚苷类物质(phenolic glycosides)浓度,增高了凝缩单宁(condensed tannins)的浓度[18]。中等浓度的臭氧处理欧洲白桦 *Betula pendula* 一个生长季节,植株体内酚苷类物质浓度降低[24];而用高浓度臭氧处理 3 个生长季节,叶片中的酚类物质总量增加,各组分的比例也发生变化[25]。高浓度臭氧还能提高欧洲白桦体内 3,4′-二氢基苯丙酮 3-β-d-葡萄糖苷(3,4′-dihydroxypropiophenone 3-β-d-glucoside)、绿源酸(chlorogenic acid)和黄酮糖苷(flavone aglycons)的浓度[26]。臭氧处理能够增强植物中与防御相关的酶类活性,调控莽草酸合成途径,酚类化合物就是由莽草酸合成途径衍生而来的[27]。不同生物合成途径对底物的相互竞争造成了植物体内酚类物质积聚量的不同[28],这一竞争又受非生物因素的影响(例如空气污染的影响)[29]。高浓度臭氧处理能够降低烟草表皮中西松烷二萜类物质(cembranoid diterpenes)的含量[30],提高火炬松 *Pinus taeda* 中的单宁浓度,但酚类的总浓度不变[31]。然而,低浓度臭氧处理不影响樟子松 *Pinus sylvestris* 针叶中酚、萜、树脂酸的含量[22]。

1.2　臭氧对植物体内信号分子以及挥发物的影响

作为植物毒性污染物,臭氧可以激活植物–病害互作信号传递途径,产生与其高度相似的防御反应[27]:表达有关防御基因、释放乙烯和其它挥发性有机化合物,合成信号分子(茉莉酸、水杨酸、乙烯等)[32]。因此,常规空气中的臭氧可以成为重要的非生物诱导子(abiotic elicitor)[33]。臭氧处理会导致水杨酸在烟草 *Nicotiana* *tabaum* 和拟南芥 *Arobidopsis* 植株中积累[34,35]。臭氧还能使长角豆 *Ceratonia siliqua*、油橄榄 *Olea europaea*、冬青栎 *Quercus ilex rotundifolia*、番茄的挥发性有机化合物(Volatile Organic Compounds ,VOCs)的总释放量增高[36,37]。不同植物及其品种对臭氧的反应不同,例如:烟草臭氧抗性品种 Bel B ,用 170nmolmol^{-1}浓度的臭氧处理后 5h ,很快释放出倍半萜类;而敏感品种 Bel W3 则在用臭氧处理后 24h ,释放出大量的倍半萜类、水杨酸甲酯和 C_6 化合物[38]。在光照条件下,烟草 Bel W3 品种大约每吸收 5 个臭氧分子,就释放 1 个分子的 C_6 挥发物[39]。臭氧对松树 *Pinus sylvestris* VOCs 释放的影响没有对烟草那么明显[38],经臭氧处理的欧洲白桦 *Betula pendula* VOCs 的释放没有变化[40]。

臭氧处理有时会诱导植物产生和害虫危害相似的化合物。臭氧处理和叶螨危害都会诱导利马豆植株释放(*E*)-4,8-二甲基-1,3,7-三壬烯、(*E*,*E*)-4,8,12-三甲基-1,3,7,11-四-十三 烯、(*Z*)-3-己烯基乙酸酯 ,但只有叶螨危害能诱导利马豆释放(*E*)-β-罗勒烯[41]。臭氧和植食性昆虫诱导植物产生 VOCs 的相似性表明,植物防御臭氧危害与产生 VOCs 吸引害虫天敌可能是适应性协同进化[41]。有人认为,从进化角度来看,VOCs 的最初功能可能是通过氧化作用而形成悬浮颗粒,以减少毒性臭氧的量[42,43]。VOCs 中倍半萜类形成悬浮颗粒的能力很强,有时达 100 %[44]。高浓度臭氧条件下,通过 VOCs 进行的信息传递会受到破坏。Janssen 等认为,从进化角度来看,植物最初产生 VOCs 并非为了吸引害虫天敌,但是一旦天敌开始对这些 VOCs 发生反应,植物就能够利用天敌间接防御害虫[45]。

1.3 臭氧对植物产量的影响

大气中臭氧水平的升高会对全球粮食产量产生不利影响。美国国家农作物损失评价网的研究表明,在大气臭氧季节平均浓度为 0.06～0.07ml/m^3 时,导致所有农作物产量降低,并且产量的减少与臭氧浓度的增加成线性关系[46]。目前空气中的臭氧的浓度已经影响农作物、森林的产量和物种的组成结构[47],并将威胁到世界的粮食生产[48]。据预测,受大气臭氧浓度迅速升高的影响, 2020 年中国春小麦和大豆的减产将分别达到 30 %和 20 %[49]。玉米在不超过 10 ml/m^3 臭氧的条件下,籽粒减少 20 %,果穗减少 32 %[46]。高浓度臭氧能够使春小麦减产达到 20 %[50]。在同样高浓度臭氧环境下,水稻叶片受害较小麦晚、发展慢;臭氧浓度增加,单株产量和千粒重下降,且小麦减产幅度大于水稻[51]。倍增浓度的臭氧处理菠菜、青菜、大豆,其生物产量和经济产量均降低[52~54]。用臭氧处理英国冬季油菜后,产量(t/hm^2)减少 14 %,种子的粗蛋白和油含量均降低[55]。

2 大气臭氧浓度升高对昆虫的影响

2.1 对昆虫生长发育的影响

臭氧能够诱导植物原生代谢和次生代谢发生数量或质量的改变,这些变化会影响植食性昆虫的取食偏嗜性、行为、生长和发育。

臭氧会影响昆虫生长发育。Trumble 等报道取食受臭氧危害的番茄植株的番茄蠹蛾 *Keiferia lycopersicella* 发育更快,但产卵量和寿命不受影响[8]。在高浓度臭氧条件下,烟天蛾 *Manduca sexta* 产卵率增加[20], 幼虫体重明显增加,存活率和生长率都提高[19]。取食芜菁 *Brassica rapa* 敏感品种的大菜粉蝶 *Pieris brassicae* 幼虫,化蛹更快,体重更重[4]。取食臭氧污染菜豆叶的墨西哥豆瓢虫 *Epilachna varivestis* 的蛹重明显大于取食未受臭氧污染的菜豆叶的瓢虫蛹重[56]。取食低浓度臭氧处理的樟子松 *Pinus sylvestris* 幼苗,盲蝽 *Lygus rugulipennis* 若虫的平均相对生长率降低,但产卵量不受影响,叶蜂 *Gilpinia pallida* 幼虫取食低浓度臭氧处理的幼苗上比取食常规空气处理的幼苗生长得好[22]。Fortin 等发现森林天幕毛虫 *Malacosoma disstria* 喜欢取食 3 倍于空气中臭氧浓度的臭氧处理的北美枫香 *Acer saccharum* ,而且发育加快[10]。森林天幕毛虫取食臭氧处理的颤杨 *Populus tremuloides* ,发育变快,个体增大,雌虫蛹重增加 31 %[18]。由于森林天幕毛虫个体大的比个体小的繁殖后代多, Percy 等推测:在将来更高浓度的臭氧环境中,这种重要森林害虫的发生会比现在更严重[6]。高浓度臭氧条件下,细蛾 *Phyllonorycter tremuloidiella* 雄虫在颤杨上发育时间增加 8 %,幼虫取食量增加 28 %,臭氧还能减少雌蛾产卵量[12]。0.1ml/m^3 的臭氧对家蝇 *Musca domestica* 的长期作用是致命的,并可使雌蝇的产卵量减少[57]。

臭氧会影响昆虫的趋性和取食偏嗜性。3 龄舞毒蛾 *Lymantria dispar* 幼虫偏嗜高浓度臭氧(15ml/m^3)处理

的白橡树,用中等浓度臭氧(9ml/m^3)处理的植物没有在常规空气中生长的植株吸引力强,从偏嗜到不偏嗜的变化出现在 6～9ml/m^3 臭氧浓度之间,而在 9～12ml/m^3 之间发生逆转[58]。在马利筋 *Asclepias curassavica* 上,3 龄帝王斑蝶 *Danaus plexippus* 幼虫偏嗜臭氧处理的叶片,而 4 龄幼虫却不表现任何偏嗜性;在叙利亚马利筋 *A. syriaca* 上,3 龄幼虫表现出偏嗜性,4 龄幼虫偏嗜未处理的叶片[21]。用 0.2ml/m^3 的臭氧对美洲黑杨进行 5h 处理后,柳蓝叶甲 *Plagiodera versicolora* 幼虫和成虫趋向于取食该植株,并且取食更多的叶片,雌成虫也更喜欢在臭氧处理过的植株上产卵[59]。墨西哥豆瓢虫对用臭氧处理的大豆叶片的趋性随着臭氧浓度的增加而增加[60,61]。随着臭氧浓度的升高,天幕毛虫对颤杨的趋性减弱,对纸桦 *Betula papyrifera* 的趋性增强[62]。高浓度臭氧条件下,细蛾 *Phyllonorycter tremuloidiella* 对颤杨的定居率降低 49 %[12]。

有些昆虫不受臭氧的影响。臭氧浓度的升高对欧洲赤松和以它为食的新松针叶蜂 *Neodiprion sertifer* 没有明显影响[63]。臭氧对生长在纸桦 *Betula papyritera* 上的毒蛾 *Orgyia leucostigma* 的生长发育没有影响[11]。Costa 等在温室和田间测定了臭氧对马铃薯 *Solanum tuberosum* 的胁迫效应和对马铃薯甲虫 *Leptinotarsa decemlineata* 的生长、产卵和存活率的影响,他们认为目前对流层臭氧的浓度,能够显著影响马铃薯敏感品系的产量,但对马铃薯上的甲虫种群没有影响[64]。低水平臭氧处理并不影响松黄叶蜂 *Neodiprion sertifer* 幼虫的平均相对生长率和成虫产卵量[22]。高浓度臭氧对大豆上玉米根叶甲 *Diabrotica virgifera virgifera* 的雌成虫的密度和产卵没有影响[65]。田间试验表明,臭氧浓度增加对其它害虫对大豆的危害没有影响[66]。

需要特别指出的是蚜虫,因为发育时间短,繁殖能力强,是研究气候变化对生物影响的最理想材料[67]。但是,蚜虫对高浓度臭氧的反应各异[68]。蚜虫对臭氧的反应取决于蚜虫和寄主植物的种类[69,70]、植物的物候学[71]、土壤营养的可利用性[58,72]和用臭氧处理时间的长短[73]。Kainulainen 等发现在高浓度臭氧环境中,蚜虫的生长发育与氨基酸的可利用性成正相关[72]。一些蚜虫在高浓度臭氧条件下生长发育更好:含高浓度臭氧的空气能够提高在挪威云杉上生长的云杉长足大蚜 *Cinara pilicornis* 若虫的相对生长率,并且蚜虫后代的累积数量也增加[74];臭氧浓度增加会刺激欧洲榉 *Fagus sylvatica* 幼苗上山毛榉叶蚜 *Phyllaphis fagi* 的生长速度[23];臭氧处理豌豆 *Pisum sativum*,会使豌豆蚜 *Acyrthosiphon pisum* 相对生长率增加 24 %[75];Percy 等发现臭氧不影响蚜虫的物种丰富度,但有利于白杨树上蚜虫种群扩大[6]。高浓度臭氧对部分蚜虫具有抑制作用:氧浓度增加的空气会抑制四季豆 *Phaseolus vulgaris* 上豆卫矛蚜 *Aphis fabae* 的生长[23];臭氧处理钝叶酸模 *Rumex obtusifolius*,酸模蚜 *Aphis rumicis* 的相对生长率降低 6 %[75];Dohmen 发现臭氧与二氧化氮的复合污染能促进大多数蚜虫的生长,但其中的臭氧有可能起负作用[76]。高浓度臭氧不仅影响蚕豆上豌豆蚜 *Acyrthosiphon pisum* 的种群大小,而且会影响其基因型和表现型的频度(genotypic and phenotypic frequencies)[77]。另外一些蚜虫则不受臭氧水平的影响:在欧洲赤松上的欧松针蚜,间断性暴露于臭氧浓度为 48μl/m^3 的空气中 4～96 h,种群取食量和数量与对照相比没有显著差异。用北美云杉上的云杉长足大蚜 *Cinara pilicornis*、云杉高蚜 *Elatobium abietinum*、欧洲赤松上的赤松长足大蚜 *Cinara pini* 做同样的实验,不管是连续暴露还间断暴露,种群取食量和数量于对照都无明显差异[57]。低水平臭氧处理樟子松 *Pinus sylvestris* 幼苗,蚜虫 *Schizolachnus pineti*、松大蚜 *Cinara pinea* 若虫的平均相对生长率不受影响[22]。

臭氧对天敌的影响目前研究还比较少,主要集中在寄生性天敌上。臭氧能够通过各种途径改变寄生性天敌的适合度。首先,臭氧可以通过改变其寻找寄主的效率而影响寄生性天敌。在高浓度臭氧条件下,膜翅目寄生性天敌的搜索效率下降,对寄主的寄生率也降低。Gate 等在室内测试了 100μl/m^3 的臭氧对寄生蜂搜寻效率的影响,实验材料是一种群集性的果蝇 *Drosophila subobscura* 幼虫与反颚茧蜂 *Asobara tabida*,发现臭氧浓度升高显著降低了茧蜂的搜寻效率,果蝇的寄生率下降了 10 %(以过滤空气为对照)。他们认为臭氧干扰了寄生蜂对对寄主的嗅觉识别,从而增加了搜索路线,降低了搜寻效率,因此大气污染很可能会减小天敌对许多害虫的控制作用[5]。其次,通过影响寄主发育,从而影响天敌的生长发育与存活。臭氧处理有利于森林天幕毛虫 *Malacosoma disstria* 的生长和发育,其天敌康刺腹寄蝇 *Compsilura concinnata* 幼虫存活率却显著下降[7]。第三,臭氧会影响植物中酚类化合物和氮素的浓度,从而影响寄生性天敌的存活率、发育、个体大小、性比、繁殖力以

及寄生的成功率[78,79]。寄主植物可以通过他感化学物质(allolochemicals)直接发生作用[80～82],或者通过降低寄主的质量间接起作用[83,84]。第四,寄主取食的植物营养下降,导致寄主的生理防御功能减弱(例如包囊作用 encapsulation),寄生性天敌的适合度则提高[85]。

2.2 对昆虫信息物质传递的影响

臭氧污染可以通过一系列因素(例如改变寄主植物品质、信息素的质量和数量、信息素的接收等)改变昆虫的行为。用臭氧对黑腹果蝇 *Drosphila melanogaster* 进行短时间熏蒸后,其聚集信息素粗提物的总量和信息素的生物活性都降低,气谱分析结果证明活性物质减少[86]。颤杨上生长的毛蚜 *Chaitophorus stevensis* 在高浓度臭氧条件下,对报警信息素的反应加强,表现为逃逸行为增强,成蚜比若蚜受臭氧浓度影响明显[87]。用性信息素诱捕云杉八齿小蠹 *Ips typographus*,在臭氧浓度高的地方日平均诱捕量较高[88]。高浓度臭氧可能会使 VOCs 的总释放量增加,激发植物释放虫害诱导化合物,但并不干扰利马豆与第三营养阶层之间的信号传递。例如臭氧处理会诱导利马豆植株释放与二点叶螨 *Tetranychus urticae* 危害相同的化合物,但其捕食性天敌—智利小植绥螨 *Phytoseiulus persimilis* 对臭氧处理的利马豆植株释放的挥发物不发生反应[41]。

3 问题和展望

研究大气臭氧浓度升高对植物及其昆虫的影响,旨在预测未来臭氧浓度升高对植物生产的影响,为制定在未来气候条件下发展农业生产的策略提供科学依据。但由于研究条件的限制,目前还存在不少问题:(1) 目前室内模拟实验研究高浓度臭氧对昆虫的影响,大部分只能从个体水平进行研究,但从昆虫个体的反应不一定能准确推测昆虫种群的反应。研究表明,在高浓度臭氧条件下,蚜虫的个体反应就不能预测蚜虫种群的反应[89]。(2) 臭氧对地下害虫影响的报道很少。(3) 由于室内实验条件的限制,臭氧对植物-害虫-天敌三重营养阶层的影响的研究较少。(4) 目前大多数研究利用开顶式气室(open-top chamber, OTC) 和开放式空气增浓装置(free air concentration enrichment, FACE) 进行的,不能完全反应高浓度臭氧条件下,自然界植物群落、天敌、共生者对昆虫行为的影响[90,91]。(5) 不少研究仅是观察臭氧对昆虫某一段时间生长发育的影响,根据这样的结果推测昆虫长期的种群变化是不可靠的。因此,需要对昆虫和植物进行几个世代的连续完整的研究,这是得出正确推测的必要条件。(6) 过去的 3 个世纪,大气温度和二氧化碳浓度一直在上升。据预测,本世纪温度将升高 2～5 ℃,而二氧化碳浓度将翻倍(由 350ml/m^3 增加到 650ml/m^3)[1]。目前已经有大量研究报道升高温度或者提高二氧化碳浓度对植物、昆虫的影响,但这两个气候变化的重要因素与臭氧联合作用对植物、昆虫影响的研究较少。

随着人类对环境问题的日益关注,高浓度臭氧对植物及其昆虫影响的研究将会越来越广泛和深入。我国这方面的研究刚刚起步,仅见零星报道,由于实验条件的限制,水平也落后于欧美国家。因此,迫切需要加强这方面的研究,积累资料,为将来制定发展农业生产的策略提供科学依据,以应对臭氧浓度升高的气候环境。

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