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•综述•

红色幼叶的适应意义探讨

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摘要: 很多木本植物的叶片会在春季和其他时期产生花青素而呈现红色, 该现象已经被众多学者所关注。本文对已有工作作了归纳总结。研究表明: 这种广泛存在的现象需要消耗营养和能量并影响光合作用, 并非只是代谢的副产品。前人以秋季红叶为研究对象, 主要提出了两大类假说: 第一类假说认为红叶是对强光、低温、干旱等恶劣环境的适应; 第二类认为红叶是植物通过化学防御警示、适口性差、隐蔽自身或暴露啃食者等方式来防御植食动物的啃食。这两类假说也都存在争议。目前对红色幼叶的研究相对较少且多侧重其作为独立视觉信号的作用, 而未能将红叶与植物的其他防御策略结合进行讨论。今后的研究应当综合环境因子的影响和啃食者的视觉分析, 并与植物其他出现红色的器官对比, 深入探讨红色幼叶的适应意义。

关键词: 红叶; 机械保护; 群落; 啃食; 权衡

A minireview on adaption of young leaf redness

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Abstract: It is well known that the leaves of many woody plant species flush red rather than green during particular stages across their life span. Non-green leaf coloration caused by active synthesis of anthocyanin in plant organs at these stages costs the plant significant resources and energy, resulting in a reduction of primary photosynthesis. Therefore, it is likely that the coloration change is an active process and not simply a by-product of metabolism. Various hypotheses formulated to explain the potential reasons for coloration change can be divided into two categories: (1) those that suggest it is physiological adaptation for resistance to severe environments (high light, drought and low temperatures); and (2) those that suggest it protects against herbivory damage (coevolution, unpalatability, camouflage and anticamouflage, etc.). To date, there is no consensus on the relative validity of these ideas. The majority of previous work has focused on only a few species and autumn leaf color change. The relatively few studies done on red young leaves in spring mostly focused on red coloration as an independent visual signal. Future studies need to consider the chemical and mechanical defense of leaf redness, as well as the anthocyanins presented in other plant organs (thorns, stems and particularly, flowers), which may experience similar selection as leaves. The quantification of environmental factors and herbivore selection would be helpful in expansion our understanding in young leaf redness.

Key words: red leaf; mechanical protection; community; herbivore; trade-off

由于叶绿素的富集, 大多数叶片都呈现绿色。然而在木本植物中, 不少种类的春季幼叶(Stone, 1979; Juniper, 1994; Dominy et al, 2002)或者秋冬季的衰老叶(Wheldale, 1925; Sanger, 1971; Lee, 2002)

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呈现红色, 这一现象很早就引起了人们的关注。

1 红叶的普遍性

秋、冬季红叶的出现绝非仅存在于少数物种中, 而是温带的一种普遍现象。根据Archetti (2009a)对全世界温带地区400个属2,368种木本植物进行统计, 其中有至少290种植物(分属于70个属)的叶片在秋季呈现出红色, 约占物种总数的12% (Archetti et al, 2009)。在个别地区例如美国的新英格兰, 红叶植物的种类甚至占当地总种数的70% (Lee et al, 2003)。

除秋叶外, 我们习见的红叶石楠(*Photinia* × *fraseri*)、桂花(*Osmanthus fragrans*)、樟树(*Cinnamomum bodinieri*)等绿叶植物的春季幼叶也呈现为红色。国外已发表的有关春季幼叶的工作目前多数集中在热带雨林(Coley, 1983; Coley & Aide, 1989; Coley & Barone, 1996; Coley & Kursar, 1996)。根据Dominy等(2002)的综述, 春季红色幼叶物种的比例在不同地区变化较大, 在7–62%之间。该文调查范围包括中美洲、亚洲、欧洲和非洲的一些森林群落, 其中亚洲和非洲的红色幼叶物种相对较多(51–62%), 而欧美则较少(7–36%)。

2 红叶的适应意义

植物学家们早就开始思考叶色变化的原因(Wheldale, 1925; Sanger, 1971; Stone, 1979; Gould et al, 1995; Lee, 2002)。前人的研究表明: 一方面可能是由于叶绿素合成或者叶绿体发育的延迟(Whatley, 1992; Coley & Kursar, 1996; Hughes et al, 2008), 使得叶片的绿色相对不明显; 另一方面可能是叶片在特定时期产生了红色色素例如花青素(Sanger, 1971; Lee, 2002), 因而显现出红色。

在传统的植物教科书中, 叶片的红色被认为仅仅只是代谢的一种副产物, 是其他色素在叶绿素含量降低时显现出来的颜色(Lee & Gould, 2002; Ougham et al, 2005)。但是研究表明, 秋季红叶的出现不仅仅是由于叶绿素的降解, 同时也伴随着红色素的合成。而合成新的色素需要消耗能量和资源, 同时叶片变红也使得植物光合效率降低(Archetti 2000; Hamilton & Brown, 2001), 植物需要付出昂贵的代价, 那么植物为什么要合成新的色素呢? 学者们提出了很多种假说来解释这一现象。Archetti (2009b)曾列举了10多种相关的假说, 大致可分为以下两类。

第一类假说认为, 叶色变红是为了应对非生物环境胁迫。例如在早期研究中, 有人指出低温环境下花青素可以将光能转化为热能以提高叶片的温度, 促进叶片的代谢活动和蒸腾作用(Oberbauer & Starr, 2002; Becker et al, 2014); 也有人提出积累花青素可以降低细胞内的水势, 提高叶片对干旱胁迫的耐受力(Chalker-Scott, 1999, 2002)。还有学者认为, 红色的多少与无机营养的水平有关(Masram et al, 2015)。在此类假说中, 光保护假说(Photoprotection Hypothesis)得到了较多的关注。Gould等(1995)提出, 花青素通过分布在叶表皮细胞中形成屏障来阻挡强光, 或者是通过中和光合作用中产生的氧自由基来降低光氧化(photooxidation)和光抑制(photoinhibition)对植物的伤害, 有利于氮元素等可流动的营养物质在老叶脱落前被回收。一些后来发表的研究也支持这一假说。如Lee等(2003)调查了美国马萨诸塞州的89种木本植物, 发现其衰老叶组织内的氮元素含量与衰老叶积累的花青素含量呈负相关, 表明红叶物种相对于非红叶物种可以更好地回收老叶中的营养; Hoch等(2003)将3种木本植物的野生型与缺失花青素的变种进行对比, 在同一物种内证实了花青素有利于氮元素的重吸收; Gould等(2002)发现含花青素的叶片虽然光和效率较绿叶低, 但是受到光抑制的影响也比较小, 而且在受到强光照射后也能更快恢复正常; Neill和Gould (2003)的工作证实, 花青素可以有效减少叶绿体产生的超氧化物; Novak和Short (2011)研究发现, UV-B对海草幼叶的花青素积累具有重要的作用。

但也有研究对光保护假说提出了质疑。Manetas (2006)指出, 花青素并不是光保护最理想的物质, 它在叶片内的分布也并不适合光保护的功能, 其他的无色类黄酮, 甚至是合成花青素的前体, 都完全可以替代它的作用; 其抗氧化的功能也仅限于叶肉细胞中含有花青素才能实现。由于适应非生物环境的假说存在一定的矛盾之处, 因此一些学者开始考虑红叶可能是动植物互作的结果。

第二类假说认为, 红叶的产生是对群落内其他生物(主要是啃食者及其捕食者天敌)的适应, 认为红叶出现的根本意义是为了降低无脊椎啃食者(主要是各类昆虫的幼虫)的伤害。不过每一种假说都有不同的侧重点。例如, 由于大部分植食性昆虫对红

色不敏感, 红色的叶片难以被啃食者发现, 由此提出了"伪装者假说"(camouflage hypothesis) (Stone, 1979; Juniper, 1993)。也有学者认为, 由于啃食者常常具有与绿叶相近的保护色, 因此红叶与之形成的强烈反差使得它们更容易被捕食者或寄生生物发现, 这就是"反伪装者假说"(Anticamouflage Hypothesis) (Lev-Yadun et al, 2004)。还有学者认为, 由于花青素具有刺激性味道, 叶片积累花青素可以防御啃食者, 这就是"适口性差的假说"(Unpalatability Hypothesis) (Coley & Aide, 1989)。在此类假说中, 由Archetti等提出的"共进化假说"得到的支持较多。他们发现, 植物叶片出现红色意味着更高的化学防御, 可以减少冬季植株上蚜虫产卵的数量(coevolution hypothesis) (Archetti, 2000; Hamilton & Brown, 2001)。蚜虫会在秋季选择合适的植物产卵越冬, 次年春天新生的蚜虫直接在产卵植株上取食。根据Ramirez等(2008)对蚜虫在山毛榉科植物上产卵行为的研究发现, 蚜虫秋季在绿叶植株上产卵显著多于同种红叶植株, 而在次年春季, 在不同颜色叶片上取食的子代蚜虫的密度差别并不明显。这表明蚜虫的偏好不是为了直接取食而是寻找更好的产卵地。Archetti (2009c)比较了野生和种植的苹果, 发现在蚜虫较多的野生植株上红叶较为常见, 而在受到人为保护的种植个体中, 红叶只有在易感染由蚜虫传播的疾病的个体上较为常见。另一方面, 具有红叶的个体果实较小, 故蚜虫倾向于在非红叶植株上产卵以获得较高的适合度。上述研究结果表明, 在叶色、抗病能力和果实大小之间可能存在权衡, 支持了红叶是一种防御信号的假说。

不论是何种内在的机制, 红叶可以有效防御啃食者这一解释获得了不少实验证据的支持(Aide & Londono, 1989; Döring et al, 2009; Holopainen et al, 2009; Archetti, 2009c)。然而这些证据也存在一定的不足。首先, 研究大多集中于蚜虫这种高度特化且运动能力低的啃食者, 其他种类是否适用该假说则不得而知; 另外, 有人提出蚜虫的眼并不具备红光受体(Döring & Chittka, 2007), 因此它对红叶的识别可能不是通过颜色而是气味。这使得防御假说面临挑战。

3 红色幼叶的适应意义

根据Lev-Yadun等(2012)通过在芬兰、日本和以色列3个地区的调查, 发现具有绿色幼叶的物种, 其老叶绝大多数也是绿色或黄色; 而具有红色老叶的物种, 其幼叶也或多或少会表现出一些红色; 而当幼叶为红色时, 则有一半左右物种的老叶还是黄绿色。这可能暗示幼叶和老叶所受到的选择压力可能不尽相同。这一规律在其他一些研究中也得到了证实(Lee & Collins, 2001; Chen & Huang, 2013)。与成熟叶相比, 生长过程中的幼叶含有丰富的营养, 同时机械组织又相对不发达, 因此更容易受到啃食者的伤害(Numata et al, 2004; Karageorgou & Manetas, 2006)。那么普遍存在的红色幼叶现象与防御啃食之间是否存在联系呢？目前还没有公认的结论。已发表的工作大都关注热带雨林的幼叶(Coley, 1983; Coley & Aide, 1989; Dominy et al, 2002), 其他地区则鲜有报道。

另一方面, 因为很多物种的叶片具有各种机械结构或附属物, 包括表皮毛、复表皮、角质层, 还有胞内草酸钙晶体等, 这些结构同样具有保护叶片的功能, 可以有效抵御啃食(Ward et al, 1997; Ruiz et al, 2002; Lev-Yadun, 2006; Lev-Yadun & Halpern, 2008)。以往的研究或单独考虑红色对于叶片的意义, 或专注于机械组织对叶片的保护, 并未将两方面联系起来。Chen和Huang (2013)对武汉地区76种常见木本植物的叶色和形态特征进行了分析, 发现幼叶在红色与机械保护水平之间存在权衡, 具有红色幼叶的物种, 在表皮毛、复表皮和加厚角质层3项特征上的水平较低, 而绿色幼叶的物种则具备更多的机械保护结构。这项工作表明, 幼叶的红色并非是独立作用的性状, 而是与其他特征共同参与防御功能。把红色和机械保护结合考虑, 可以更准确地理解幼叶红色的适应意义。

为进一步研究红色幼叶的意义, 笔者认为应该从下面几个方面入手: (1)明确有哪些因素会影响红叶的出现。前人的研究已经涉及到各种生物和非生物因子(Archetti et al, 2009), 但是多数工作都集中在一个或少数几个物种, 其研究内容也多为提出或验证某类假说(Ougham et al, 2005; Karageorgou & Manetas, 2006; Hughes et al, 2007; Karageorgou et al, 2008)。几种假说都得到了一些支持。近年来, 有学者提出红叶的出现可能是多种选择压力作用的共同结果, 多种假说可以同时成立(Lev-Yadun, 2009)。这种观点在一定程度上可以解决目前争论不

休的局面, 但是也让问题变得更加复杂, 以往对少数物种的研究结果可能不具备广泛的意义。因此, 在较大尺度上选取更多的物种来进行相关因素的定量分析也许是一种可行的思路。即可以选取不同地区和不同群落, 对植物特征和环境因子进行测量。例如, 测定光照、土壤湿度等环境参数, 同时调查啃食水平和啃食者种类, 比较这些参数在不同的群落环境中的同种个体之间存在哪些差异, 以及这些差异是否与红叶的表达水平有关, 然后用相关性分析找到可能的相关因素, 再利用多元回归分析同时建立线性回归和非线性回归的模型, 以推测这些因素之间较为合理的关系。也可以比较不同群落中的同一物种, 利用多因素方差分析找出在不同地区对叶色影响较大的因素; 或者从年际变化入手, 长时间跟踪监测气候指标(如有效积温、年降水量等)的变化, 分析其是否会引起次年红叶水平变化; 或者通过人工控制, 一方面模拟不同的啃食程度研究其对叶色的影响, 另一方面也可以通过改变叶色来研究其对植物受啃食程度的影响等等。

在探究红叶适应意义的同时, 另一个重要的问题就是人类所观察到的红叶是否也能被啃食者所感知。虽然不少的学者都支持红叶可以抵御啃食, 但是有一个基本的前提至今也未能得到直接的证据支持, 那就是啃食者(主要是无脊椎动物)能否从视觉上区分红叶和绿叶呢？前文提到蚜虫无法感受红光信号, 在后来的工作中(Döring et al, 2009)虽然推测可以通过对红色和黄色的敏感差异来识别红色, 但缺少直接的证据。近年来, 越来越多的学者开始关注昆虫和人类的色觉差异(Döring & Chittka, 2007; Pegram et al, 2013; Whitney et al, 2016)。借助于便携式光谱分析仪, 我们可以针对啃食者建立类似人类三原色的色觉模型, 量化分析啃食者对不同颜色的感知差异(Chittka & Kevan, 2005)。根据啃食者的色觉敏感区域，对群落中不同植物红色和绿色幼叶进行量化并比较其差异, 可以提供直接的证据。

除了在大尺度上的分析, 也可以从个体水平入手。有研究发现, 在同种个体之间甚至同一个体的不同叶片, 花青素的含量并非完全一致(Schaberg et al, 2003; Lev-Yadun, 2007; Cooney et al, 2012)。对此, 可以利用图像和色彩分析软件对同种内个体或叶片的颜色进行定量, 或者以某种植物为对象建立种内叶色梯度, 探讨其与被啃食程度是否相关。

除此之外, 在已有的工作中虽然发现幼叶在红色和机械保护之间具有一定的权衡, 但是这种权衡目前还表现在种间水平。那么这种权衡在种内是否也存在呢？可以通过选取一些个体间变化较大的物种, 对红色和机械保护特征进行定量分析, 更细致地探讨两者之间的关系。

此外, 花青素作为广泛分布于植物各器官(茎、叶、花、果等)的一类色素, 它的作用也是多重的: 例如花冠和成熟果实中的花青素可以有效吸引传粉者和种子传播者(Hoballah et al, 2007, Glover, 2011); 在叶片中的花青素除了上述功能之外, 有学者发现囊距紫堇(*Corydalis benecincta*)可以生成花青素来模拟周围的岩石环境以减少啃食(Niu et al, 2014); 还有学者发现植物茎可以用花青素作为棘刺的警戒色(Lev-Yadun, 2001; Ronel & Lev-Yadun, 2012)或模拟棘刺(Lev-Yadun & Gould, 2009)。综合花青素的多种功能也许有助于更准确地评价红色在幼叶保护过程中贡献的大小, 同时也可以为春季植物保护、防止虫害提供理论依据。

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