

溪流粗木质残体的生态学研究进展

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摘要:粗木质残体(CWD)是森林或溪流生态系统中残存的超过一定直径大小的站杆、倒木、枝桠及根系等死木质物的总称, 溪流 CWD 对于溪流生态系统的稳定、水生生物多样性、河槽形态及其变化过程有着重要的作用。对溪流 CWD 的产生和分类, 溪流 CWD 贮量、分布和动态, 以及溪流 CWD 的功能和管理分别进行了总结。并指出应尽快在国内开展溪流 CWD 的研究和管理。

关键词:粗木质残体; 倒木; 溪流; 河岸带; 管理

Advances in Ecological Studies on In-stream Coarse Woody Debris

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Abstract: Coarse woody debris (CWD), mainly found in the forms of snags, fallen wood, large branches, twigs and roots with diameter more than a certain value in forest ecosystems or stream ecosystems, it was often neglected as an ecological component in studying and managing many terrestrial and aquatic ecosystems. In forest ecosystems, CWD has many crucial ecological functions such as habitat for organisms, a site for nitrogen fixation, energy flow, and nutrient cycling. Management of streams, lakes, and wetlands in forested ecosystems or watersheds represents one of the most revolutionary changes in forestry in the latter half of the 20th century, and so, today, there is widespread agreement that historical forest practices negatively altered the structure of the aquatic ecosystems and decreased their productivity. Along with the continuous development of researches on stream ecosystems and watershed ecology, the intercross and combination of terrestrial ecosystems and aquatic ecosystems researches are a new current in studying ecosystems. Therefore, although a study on CWD is an important aspect in traditional forest ecology, increasingly more ecologists pay their attentions to in-stream CWD and are aware of the important effects of in-stream CWD in basic study and practical management. While CWD in forest ecosystems turns into stream ecosystems because of natural power or human power, it is turned into in-stream CWD. In-stream CWD is one of the most important and intuitionistic input and disturbance of terrestrial ecosystems on stream ecosystems, and it is a major connection between terrestrial ecosystems and stream ecosystems. In-stream CWD also plays an important role in stabilizing stream ecosystem, aquatic biology diversity, and channel morphology and its change process.

In this paper, based on a mass of literatures about CWD, the formation and classification of CWD in streams, storage, distribution, trends and its function and management have been summed up, respectively.

基金项目: 中国科学院知识创新工程项目(KZCX2-406)、国家自然科学基金(39970123)和长白山开放站基金资助项目
本文在撰写过程中得到美国 Purdue 大学林学与自然资源系邵国凡教授及吴文春博士的帮助, 特致谢忱。
收稿日期: 2001-01-31, 修订日期: 2001-11-02
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ly, and most of these related researches have been commented. We also pointed out that, although the research on in-stream CWD did not have a long history, it becomes more and more important in the relative studies and managements. In China, the relative researches have been mainly focused on CWD in forest ecosystems and litter in aquatic ecosystems from forest ecosystems, and they are far from sufficient. Therefore, it is important and imperative to develop researches and managements on CWD in streams quickly in our country.

Key words:coarse woody debris; fallen wood; stream; riparian; management

文章编号:1000-0933(2002)01-0087-07 中图分类号:S718.5 文献标识码:A

粗木质残体(Coarse Woody Debris,简称 CWD)^[1~4]是森林生态系统(Forest ecosystem)或溪流生态系统(Stream ecosystem)中残存的超过一定直径大小的站杆(Snag)、倒木(Fallen wood)、枝桠(Branch and twig)及根系(Root)等死木质物的总称。一般地,直径大于 2.5cm 的木质物称为 CWD,较小的则归为枯枝落叶(Litter)^[1,3]。尽管 1925 年 Graham^[5]曾指出“倒木(Fallen trees)是森林生态系统中的一个生态单位(Ecological unit)”,强调倒木的生态功能;但直到 20 世纪 70 年代,木质物残体才真正被认为是森林生态系统中的一个生态单位^[3]。1986 年《Advances in Ecological Research》第 15 卷关于“温带生态系统中的木质物残体生态学”一文^[1]的问世,不仅对以前的研究工作进行了系统的总结,而且为今后的相关研究奠定了理论基础^[3]。

20 世纪后期,森林生态系统中溪流、湖泊和湿地的管理是林业上最具革命性的变化和进展之一^[6];过去不适当的森林经营对水生生态系统(Aquatic ecosystem)结构的负面影响和导致其生产力降低^[7~9]这一观点如今已被人们普遍接受^[6]。随着河溪生态系统^[10~12]和流域生态学(Watershed ecology)^[13~15]研究的不断发展,水陆生态系统研究的交叉与结合已成为生态系统研究的一个新趋势^[13~15]。因此,尽管 CWD 研究传统森林生态系统研究的一个重要方面,越来越多的生态学者将研究对象转为森林溪流中的 CWD,溪流 CWD 研究在基础理论和管理实践上的作用日显重要。

1 溪流粗木质残体的产生和分类

森林生态系统中的粗木质残体因自然力或人力进入溪流生态系统后,就成为溪流粗木质残体,它是陆地生态系统对水生生态系统最重要、最直观的输入和干扰之一,也是陆地生态系统与水生生态系统之间的主要联结。

林地特别是河岸带(Riparian)中的死木质物产生后,一些直径较小的粗木质残体往往会因重力、风力的作用或随地表径流进入溪流生态系统。此外,紧邻河岸边的树木由于枯倒、风折或河水对河岸的冲蚀而以大倒木的形式进入溪流成为残体坝(Debris dam^[16,17])。一些动物和人类活动也是溪流粗木质残体形成的重要原因,如河狸筑坝或人类砍倒树木作为渡桥等。虽然有研究^[18,19]对进入溪流的森林凋落物中枝、叶数量进行了测算,但目前仍很难准确地估算不同原因形成的溪流粗木质残体在总量中分别所占的比例;溪流粗木质残体总量占林地或河岸带所产生的粗木质残体总量的比例将是一个重要的指标,当然这建立在对溪流 CWD 和林地 CWD 总量准确估算的基础上。

溪流 CWD 的最小直径与林地 CWD 的标准一样,都是 2.5cm;直径是 CWD 研究中的重要指标之一,在不同的研究中可根据所调查 CWD 的径级分布分为不同的类别。其中,直径大于 10cm 的 CWD 又称为大木质物残体(Large Woody Debris,简称 LWD)^[20~23],由于具有较大的直径和长度,LWD 往往成为残体坝。Gregory 等^[16]在对 Lymington 流域部分河流残体坝的研究中,把残体坝分成 3 种类型,即活动型(Active debris dam)、完全型(Complete debris dam)和部分型(Partial debris dam)。其中,活动型残体坝在整个河槽横断面阻水并在顺水流方向形成长台阶,完全型残体坝也是整个横断面阻水但不形成台阶,部分型残体坝只阻塞河槽的部分横断面^[17]。

CWD 开始不断地分解腐烂,释放和归还养分,因此,划分倒木腐烂级是进行倒木养分的基础。1972 年,Fogel 等在研究中根据其外表特征,提出划分倒木腐烂级的 5 级划分系统^[24];随后,一些学

者如 MacMillan^[25]、Maser 等^[26]发展和完善了该系统。表 1 引自 Rikhari 等^[27]的研究,它详细说明了该分类系统。此外,Lienkamper 等^[20]在研究中对 Fogel 的划分系统做了一些改动,把 CWD 按腐烂情况分为 4 级,其中单独把活的倒木作为一级。

表 1 CWD 的 5 级分类系统
Table 1 A 5-class system of decay for coarse woody debris

| 评价指标 Parameters | 腐烂级 Decay classes | | | | |
|-----------------------|-------------------|-------|-------|-------|----|
| | I | Ⅱ | Ⅲ | Ⅳ | V |
| 树皮覆盖率 Bark cover (%) | >95 | 75~95 | 25~75 | 5~25 | <5 |
| 树皮上的苔藓 Lichen on bark | 存在 | 存在或无 | 无 | 无 | 无 |
| 边材 Sap wood | 完整 | 部分变软 | 腐烂但存在 | 完全腐烂 | 无 |
| 芯材 Heart wood | 完整 | 完整 | 完整 | 结构不完整 | 无 |
| 树皮 Bark | 完整 | 完整 | 脱落 | 脱落 | 无 |
| * 小枝 Twigs (>3cm) | 存在 | 无 | 无 | 无 | 无 |
| 大枝 Branches | >1m | <1m | <0.5m | 残存 | 无 |

* 该项指标仅适用于倒木 This parameters are fit for fallen wood

2 CWD 在溪流中的贮量、分布与动态

CWD 在森林生态系统养分循环中的一个重要作用是在系统遭受重大外界扰动后贮藏养分和增加系统稳定性^[28],因此,CWD 在森林生态系统中的贮量、分布与分解动态一直是森林生态系统 CWD 研究的重要内容。另一方面,基于 CWD 对河床形态、河槽变化过程和河流生态环境的影响,可假设自身静止的 CWD 或有机质积聚物会引起河槽的动态变化^[17];因此有必要了解河道中 CWD 形成的残体坝的持久性,包括 CWD 积聚、存留、腐烂分解的平衡以及可能的变化^[17]。对于溪流中的 CWD 而言,其生物量取决于输入、分解速率和在溪流中的移动过程等因素^[29];气候、土壤、溪水的流速、地形、坡度、河床宽度、林龄、林分密度和森林群落的组成等共同决定 CWD 在溪流生态系统中的总量和分布^[1,27,29~31],有时大的洪水会导致河岸带树木死亡从而增加溪流中的 CWD^[32]。人类活动可以显著改变林分向溪流输入的 CWD 总量^[1,33,34],如森林砍伐可以在初期增加向溪流输入的 CWD 总量^[30],但在更长的时间尺度上因为河岸带树木的损失,砍伐会减少向溪流输入的 CWD 总量^[1,35,36],在一些河流,人类将 CWD 从其中清理出去会直接影响 CWD 在河流中的贮量^[33]。

对于河道中 CWD 现存量的研究一直溪流 CWD 研究的重点和基础。Harmon 等指出,在无管理或干扰的河道中,CWD 重量和体积的变化范围分别为 1~1800mg/hm² 和 2.5~4500m³/hm²^[1]。Rikhari 等在中部喜马拉雅地区两条河流的研究^[27]表明 CWD 含量在 9.42~35.3mg/hm² 间;Triska 等^[37]研究认为在一级支流中的 CWD 可达 420mg/hm²;Lienkaemper 等在 Oregon 的研究^[20]认为 CWD 现存量的变化范围是 230~750mg/hm²,而从森林到溪流的输入是每年约 2~8.8mg/hm²;Hedman 等在南部 Appalachian 山区流域的研究^[23]结果是木木质残体可高达 3.6~13.2kg/m²。溪流 CWD 贮量和河岸带森林的状况有着密切的关系,Hedman 等^[23]研究了河岸带森林的演替阶段与溪流 CWD 的关系;Triska 等^[37]曾假设在 Oregon 河流中 LWD 贮量随时间而线形增加,到 450~500a 时达到最大;Spies 等^[30]认为大的干扰后 500a 内 LWD 贮量曲线呈 U 型,超过 500a 后下降至中间水平,在干扰后 1000a 达到稳定状态。类似的关于河岸带森林受到干扰或砍伐后溪流中 CWD 贮量变化的研究^[38~42]较多,一般的结论^[38,43]是河流将随着森林的退化、积聚和恢复 3 个阶段,在较长时间后才重新达到稳定。

CWD 在溪流中的分配不是平均的;Rikhari 等在中部喜马拉雅地区两条河流的研究^[27]表明,CWD 贮量在河流两岸都是从底部到顶部下降的;尽管 CWD 的容积和生物量之间存在紧密的关系,但对于某些地方而言,存在容积较高而生物量较低的情况,这是由于倒木腐烂情况不同而导致密度的差异造成的^[27]。溪流 CWD 的数量和贮量在不同径级的分布存在显著的差异,随着径级的增大,CWD 的数量下降,表现出与林地活木相似的倒 J 型关系^[25,27]。尽管较大径级的 CWD 数量较少,但由于径级增加、体积增大而往往使

大径级 CWD 处于主导地位。一般地,随着径级的增加,CWD 表面积与体积之比下降^[27],这一比值常用于解释 CWD 的分解过程和养分转移速度^[44,45],径级较小的 CWD 一般有着较大的表面积与体积比,从而分解较快^[27]。另外,研究^[27]还表明,径级较小的 CWD 一般有着较高的 N 含量,较低的 C/N 比和木质素,这也利于其分解。

CWD 在河流中的分解过程中,有机质从残体坝中的流失方式是多样的,测算其流失量也非常困难,在目前文献资料中很少有明确的指标^[17]。Anderson 等曾测算过有机质年输入量的 60%~70% 会存留在残体坝中足够的时间以供各种微生物利用^[46]。其他一些研究表明,在较短时间内,溪流 CWD 的贮量或分布会发生较大的变化;如在英国新林区,沿苏格兰高地水系约有 1/3 的残体坝在 12 个月内会发生变化^[16],在加利福尼亚,CWD 在 6a 内约 65% 会重新分布^[17]。而另外一些研究则表明,形成残体坝的 CWD 的驻留时间要长得多,Sedell 等进行的一项调查^[26]指出这种驻留时间长达 200a。以地貌学为基础对 CWD 的积聚和腐烂做出平衡计算是很必要的^[17];在这方面,Harmon 等 1986 年已提出了有用的研究结果^[1],Cummins 等回顾了河流生态系统有机物估测方面存在的问题^[47]。

3 溪流 CWD 的功能及其管理

国外和我国长白山^[3,4,28,48,49]的大量研究表明,CWD 是温带森林生态系统的重要组成部分,CWD 的存在,给森林生态系统增添了结构和生境多样性、生物多样性和功能多样性^[4]。对于溪流生态系统而言,CWD 同样是其中的一个重要组成部分^[23],因为大多数河流内的有机质来自外部,其生态系统净产出通常是负的^[50],故碎屑腐质是河流生态系统动力的重要源泉,CWD 也就是其重要的外界输入,CWD 分解可不断地向河流中释放营养物质。这里得指出的是河流连续体概念(River Continuum Conception, RCC)^[12]中的一个观点,即下游河段(较高的支流级数)在一定程度上依赖于上游(较低的支流级数)的低效率;在上游,C 的摄入主要来自河岸带,在河流中部,伴随着河岸遮蔽物的减少,水较清澈,内部生产是分解碳化合物较主要的来源,在流域下游的大河中,来自支流以及周期性淹没的洪泛平原的累积充填物成为主要的碳源。

作为溪流生态系统的主要输入,CWD 对于溪流生态系统的稳定具有重要的意义。Golladay 在 1988 年就森林破坏后对河流中营养物质的影响进行了研究^[51],结果表明:植被破坏后,溪流中 CWD 的输入减少,虽然它和参照基准河流在 K、Ca 和硫酸盐保有量方面无差别,但 N 和 P 的保有量比基准河流低,而 CWD 形成的残体坝处是吸收磷酸盐的主要场所;Webster 等的研究^[43]也证实了该观点。此外,溪流 CWD 还具有以下功能^[17,23,52~54]:(1)影响汇流,尤其是洪峰流向以及沿河的泥沙输送和蓄积;(2)CWD 的聚集可改变河槽侵蚀和水流势能的沿程分布;(3)对溪流生态环境有影响,因为 CWD 的积聚会改变水生生物栖息地的多样性和生物的数量。

由于 CWD 在溪流生态系统中的存在,往往会对航运和某些生物(如鲑鳟亚目鱼类^[55,56])有不利影响,所以清理河道中的 CWD 在过去成了惯例。而随着对溪流 CWD 研究的深入和其功能的了解,清除 CWD 的不利后果已为公众所认识;在河槽里清除大量的 CWD,其初期的明显后果就是洪峰沿主河槽的演进发生变化,特别是中小流量的洪峰,其流速可快 2~3 倍;而大洪峰流量时由于 CWD 易被冲走,受到的影响则较小^[17]。要说明清除 CWD 对河道中泥沙运动所产生的影响^[17,53]还比较困难,但调查中下面一些迹象是很明显的^[17]:水流携带的泥沙增加,沿途的沉积量减少;浅滩深槽中的水不如以前清澈透明;局部河岸的冲蚀加重,导致河槽中水生生物栖息场所的多样性减少。

河流的管理和保护有着重要的意义,尤其是为了了解河流的中短期动力特性和保持栖息地的多样性,这需要不断加深对 CWD 的作用和动态的认识,进而采取科学合理的溪流 CWD 管理措施。目前一些地方还是采用传统的彻底清除的办法,这显然是有待改进的。一种新的管理策略应该是将它们分类,有选择地清除一部分,以求达到最有效地保护栖息地的目的;要达到这个目的,可以在一些地方应用 Swanson 等^[57]提出的河岸管理单元,并将其作为管理策略的一个组成部分^[17]。这个管理单元策略要结合有机质输入、留存和流失的动态模型来设计,目标是使沿河槽水流能量的变化达到最小。

4 结语 万方数据

总之,溪流 CWD 对于溪流生态系统的稳定、水生生物多样性、河槽形态及其变化过程有着重要的作

用。在温带河流中这类积聚物的动态特性就是变化频繁,随季节而变化,并与河岸带树木的特征有关。在制订相关管理策略时应当把 CWD 看作是整个系统不可缺少的一个部分;要认识到应该避免过多清除,因为这会引洪水流量加大、流速加快,进而导致河槽变化,减少环境多样性;而对河道中的 CWD 进行有选择的清理和经常性的维护则有利于保持河槽的稳定。

自从人们意识到 CWD 在生态系统中的重要性并开展溪流 CWD 研究以来,溪流 CWD 的研究一直是溪流生态系统研究或水陆复合生态系统研究的一个重要内容,至今都吸引了许多学者的研究兴趣^[58~60],甚至把该内容作为一门新的交叉学科来看待^[58]。但国内在这方面的工作几乎是空白,相关的研究主要是长白山森林生态系统中的 CWD 研究^[28,48,49]或河岸带凋落物在水体中的数量和动态。因此,有必要开展溪流 CWD 的生态学研究,这将有助于深化人们对 CWD 的研究以及详细了解森林生态系统与水生态系统之间的相互作用,对于研究物质在流域生态系统中循环过程和水体生产力以及水生生物多样性也大有裨益;而在相关研究基础上进行的合适的管理措施对于维持溪流生态系统的稳定和保护其生物多样性无疑是有用的。鉴于我国很多地区存在水资源短缺、水质恶化严重、物种急速减少等生态环境问题的现状,开展溪流 CWD 的研究和管理更有着十分重要的意义。

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