ISSN 1000-0933
CN 11-2031/Q

生态学报

Acta Ecologica Sinica

第 32 卷 第 5 期 Vol.32 No.5 2012

中国生态学学会
中国科学院生态环境研究中心 主办
科学出版社 出版

中国科学院科学出版基金资助出版

生 态 学 报

(SHENGTAI XUEBAO)

第 32 卷 第 5 期　　2012 年 3 月　(半月刊)

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专论与综述

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期刊基本参数:CN 11-2031/Q * 1981 * m * 16 * 308 * zh * P * ￥70.00 * 1510 * 35 * 2012-03

封面图说:气候变暖下的北极冰盖——自从 1978 年人类对北极冰盖进行遥感监测以来,北极冰正以平均每年 8.5% 的速度持续缩小,每年 1500 亿吨的速度在融化。这使科学家相信,冰盖缩小的根本原因是全球变暖。北极的冰盖消失,让更大面积的深色海水暴露出来,使海水吸收更多太阳热辐射反过来又加剧冰盖融化。由于北极冰的加速融化,北冰洋的通航已经成为 21 世纪初全球最重要的自然地理事件和生态事件。从这张航片可以看到北极冰缘正在消融、开裂崩塌的现状。

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DOI: 10.5846/stxb201012231832

刘斌,潘澜,薛立. 台风对森林的影响. 生态学报,2012,32(5):1596-1605.

Liu B, Pan L, Xue L. A review of the effect of typhoon on forests. Acta Ecologica Sinica,2012,32(5):1596-1605.

台风对森林的影响

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摘要:台风通过树枝折断、吹落叶果、产生倒木和折干等许多途径影响林分结构和动态。森林受害程度随树种、林龄、森林类型、树高和地形而异。高密度的森林通常具有较差的根系和较大的树高/胸径比值,在台风袭击下,往往具有较高的受损和死亡的风险。台风疏开郁闭的林冠层,促进了先锋树种的大量增加、生长和成熟,形成的林隙也为个体更新提供了机会。强风造成了土壤基质的多样化, 从而促进了实生苗和幼树的更新和生物多样性的增加。台风也通过改变粗木质残体,枯枝落叶层,地洞和土墩,以及繁殖可用性来影响生物多样性。台风产生的粗死木和枯枝落叶使森林的碳储量迅速归还土壤,并影响土壤的养分分布。台风减少了动物的食物供应和恶化栖息地的环境,减少鸟的数量,促进昆虫扩散。受害森林给害虫滋生提供了场所。今后的研究热点是受台风干扰森林的长期监测,不同森林土壤的有机碳贮藏,土壤和养分流失规律,台风和其他自然灾害的交叉影响,改进数学模型以准确预测台风损害。

关键词:台风;森林;生物多样性;土壤;动物

A review of the effect of typhoon on forests

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Abstract: Typhoons are one of the most important natural disturbances, which affect forest stand structures and dynamics in various ways such as by snapping branches, stripping leaves and fruits, uprooting trunks and breaking stem. Many factors, such as position in canopy, soil conditions, stage of growth, physiognomy, affect wind resistance of tree species. Moreover, there is a wind velocity beyond which all species are affected by the sheer magnitude of the wind's kinetic energy. Therefore, forest damage varies as a function of tree species, tree age, forest type, tree height and topographic location. High density forests often suffer great damage and mortality due to their relatively weak roots and a high ratio of tree height to diameter at breast height. In forest ecosystems, typhoon disturbance is one of the major agents generating a mosaic of heterogeneous habitat patches at various spatial scales. Canopy gaps caused by typhoon disturbance can occur in a variety of sizes, from single fallen trees to large-scale blowdowns, which is important factor affecting species composition and some critical ecosystem patterns and processes such as understory light environments, and nutrient cycling, and have major effects on patterns of forest regeneration through differential effects on tree species and impacts on resource availability. Light increases due to canopy gaps and soil nutrient availability in the understory also increases due to a decrease in uptake by disturbed canopy trees, which can promote the immigration of early successional species. Moreover, species richness is affected by coarse woody debris, litter layer, pits, and mounds, and the availability of propagules. Coarse woody debris and litterfall caused by typhoon promote return of forest carbon to soil, and affect distribution of soil nutrients. Typhoon disturbances can return large amounts of plant material into the forest floor. Litterfall, particularly green leaves resulting

基金项目:广东省林业局资助项目(F09054)

收稿日期:2010-12-23; **修订日期**:2011-04-14

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from the typhoons have higher nutrient concentrations than the normal litter for the nutrients that are translocated during senescence. This leads to an increase in nutrient availability and in soil after typhoons. The nutrient released from the rapid decomposition of fresh leaves might exceed the capacity of the vegetation, microorganisms, and the soil to retain the nutrients in the ecosystem, with nutrient transfer patterns of rapid loss for nutrients. Typhoon affects the animals by reducing food availability and deteriorating habitat, The passage of a typhoon can kill birds owing to exposure to wind and rain, particularly those vulnerable to wind and rain prior to the storm. Typhoon affects insect population numbers and causes local extinctions or dramatic outbreaks of populations through effects on either food sources and/or predators, it also damages forest place for pest propagation. Future research of typhoon effect on forests will focus on developing long-term monitoring of forests with typhoon interference, researching organic carbon storage of different forest soils, erosion patterns of soils and nutrients, intersection effect of typhoon and other natural disasters, improving mathematical models for forecasting typhoon damage.

Key Words: typhoon; forest; biodiversity; soil; animal

台风(美洲称为“飓风-Hurricane”)具有降雨强度大和风速快的特点,通过风的水平力和树本身重量产生的垂直重力作用于树木,可以造成大径级个体严重受损,产生树皮撕裂、折干、枝条折断、大量落叶、连根拔起[1-2]和种实早落,甚至会引发和传播病虫害[3],也可以通过产生的倒木、断枝和落叶压倒其它植株,引起小面积范围内的个体死亡[4],产生大量的林窗,导致郁闭度减少、透光性增强、引起生境异质性,影响森林生态系统的初级生产力、水文特征、养分循环、植被更新、动物群落演替、群落内的物种组成和结构以及生态系统的稳定性等[5-7]。许多学者研究了台风对森林生态系统的影响,内容集中在植被动态、森林林冠和密度[8-13],森林群落机械损伤[14]、凋落物特征[15]、水文功能规律[16-17]和土壤流失量[18]等方面。当前,台风频繁出现,本文就台风对森林的损害、台风后森林恢复和对森林土壤的影响进行综述,可以为受台风损害森林的恢复和管理提供参考。

1　台风对森林的损害

台风通过增加乔木层树木的翻折等许多途径影响林分结构和力学特征[19-20]。风速是决定破坏严重程度的主要因子,台风使树木的受损程度和对森林生态系统的影响随着风速的增加而线性增加[19]。树木的生物学特性(如树龄、树木高度、树冠大小)、树木位置以及林分疏密度等因子都会影响森林遭受台风损害的形式和程度[19,21]。森林遭受损害的程度与林分年龄和高度为正相关关系[22]。胸径、树高与风害的发生有着密切的关系。由于树冠周围的风速随着高度的增加而增加,并且高大树木的林冠暴露在高速风中的面积较大,所以常比低矮的树木有更大的受害和死亡的风险[23-26],而一些较矮的树木受到高大树木林冠的保护[27]。另外,树木的刚性随着高度增加而增大,致使高大树木受损增加[28],而比较小的幼龄树在一定的风速下更具有柔韧性[29]。在美国佛罗里达州东南部的红树林经历安德鲁台风后,较大胸径树木的死亡率和枝干折断数量比较小胸径的树木更大[30],成熟森林有很高的茎杆的折断率[22]。强风倾向于选择性地除去森林中树龄最高、树体最大的树木。Foster 研究台风对于美国新英格兰中部地区森林植被的影响时发现,生长较快、构成树冠最上层的先锋树种,如杨树(*Populus* spp.)、北美乔松(*Pinus strobus*)、美国赤松(*Pinus resinosa*)和北美桦(*Betula papyrifera*)比那些生长较慢、在最高树冠层以下的一些树种,如山核桃(*Carya* spp.)、北美红枫(*Acer rubrum*)、黑桦(*Quercua alba*)和黑栎(*Quercus velutina*)更容易遭受严重的破坏[22]。成熟林更容易受台风危害,树木往往被连根拔起和树干折断。如新英格兰中部地区的森林遭受的风害随着林龄的增加而增大[31]。风速强烈影响那些比邻近树木的要高的树木[32],随着林分高度一致性的增加,风害发生的概率降低[33]。此外,与森林边缘距离的远近也影响树木受风害的可能性[34]。台风往往对林冠造成严重损坏。Shimizu[35]发现在小笠原群岛的松树木荷混交林中,台风引起约 60% 的林中空地。在 1991 年台风在波多黎各森林中引起 30% 的林木折断、连根拔起或倾斜,84% 的林木树冠受损[36]。

台风对森林的危害随树种而异。具有软木质。叶片重构能力低[29]以及浅根系的树种通常遭受很大的破坏,死亡率较高[37-38],因而阔叶树扁平而柔软的叶子比松树的针叶更容易受到风力的影响,前者浅而散开的根系增加了在台风中的倒木根拔[39]。但是在尼加拉瓜的东南沿海,1988 年的台风琼对松树林造成的损失比热带雨林更大[40-41]。

树木的抗风能力取决于木质强度、树冠形状和大小、树木大小、树干的形状、树叶特征以及根系性状(根系范围和深度)等多种因素的复合作用[28],因而树木忍受台风危害的能力和死亡率随树种而异[42]。Duryea 等[43]将波多黎各和佛罗里达州的城市森林树种分为四大类:最高抗风树木、中高抗风树木、中低抗风树木和低抗风树木。

森林密度控制森林结构的特征,尤其是乔木密度可以影响森林对台风的抵抗力。高密度的森林通常具有较差的根系状况和较大的树高/胸径比值,在强风袭击下,往往具有较高的受损和死亡的风险[44-45]。因此,间伐能够减小森林密度,促进侧根的生长,使根的固着力加强[46],从而减小台风对树木的损害。也有研究表明,间伐引起森林密度的降低会增大受损风险[31,47],原因是未经过间伐林地密度大,树木林冠摇摆的幅度受到一定限制[48],因此风害更频繁地发生在经过间伐的低密度森林[49-51]。所以,通过间伐实现侧根固着力加强而又不会增大受损风险的密度较为理想。

台风能减少乔木密度和地上生物量[52-53],但是否会减少断面积视台风的强度和树木的死亡率而定。灾难性强风后,受损森林几年内能够显著地增加小径级树木数量,影响树木径级分布。1932 年,经历台风圣西普里亚诺后的成熟松林的断面积和森林密度减少[54],几年后乔木密度、生物量和断面积迅速增加。台风发生 15 a,乔木密度达到高峰,断面积和地上生物量达到稳定状态。此后,森林死亡率提高和密度下降,使幸存的树木生存空间增大,进入断面积和生物量增加的阶段。

地貌、立地、土壤条件的特点等诸多因素在台风对林木造成的影响中有重要作用。在高海拔、迎风面、接近溪流谷底的土壤潮湿处和暴露于强风中的突起山脊处的树木损害较大[38-39],所以在高海拔和近河谷处形成较多的林隙。Bellingham 发现,台风过牙买加的热带森林后,在迎风的南坡和山脊受害严重,而背风的北坡受害较轻[55]。台风经过线路的两旁森林断枝率高,带来大面积的结构性损伤[56-57]。

地下水位深度对于能抵御折断弯矩作用的树木根系很重要[44,58],因为根系固着力的大小依赖于土壤干燥程度。台风发生时,土壤干躁地点的树木根拔很困难,更容易出现茎干折断现象,而生长在潮湿土壤上的树木往往被连根拔起[32,38-39]。在寒带森林地区如芬兰,冰冻结的土壤减少了树木根拔,但随着霜冻层深度的减少,树木变得更容易倒伏。所以台风在潮湿的土壤条件下更可能对树木产生危害,另外矿物质含量高的土壤易发生风害,而有机质含量高的土壤则不易发生[32,44]。暴雨的路径[59]和时间[60]影响台风的产生,也是台风破坏树木的关键因子。

2 台风对森林恢复的影响

台风对森林生态系统的组成结构、物种的多样性以及生态功能造成深远而复杂的影响。台风引起的强烈且是瞬时的干扰能在短时间内大规模改变整体森林结构,使之产生长期和不可逆的改变[61]。在海南岛的热带雨林中,达维台风发生 9 个月后,乔木层多样性和均匀度降低,幼树层和下木层多样性和均匀度稍微升高[4]。台风引起的森林受损的恢复途径和机理与树冠受损严重程度直接相关, 并受到光和水分条件的影响。残留植物及时开花结果和充足的土壤种子库对森林植被恢复具有促进作用[62]。台风可以导致林内生长环境的显著改变[49,63],如树木的根拔和茎干折断,林冠疏开,林窗面积大幅增加,透光性增强[60],林下植株得到的光照量显著上升,土壤养分利用的有效性增加[64-65],从而增加了森林群落的空间异质性[39,66],促进早期演替物种进入林分[67]。强光照下,树叶容易受光抑制影响,其忍受程度随植物种类而异[68-69]。在光照充足并充满竞争的林分间隙下,耐荫树木的幼苗快速适应环境、降低现有遮阴叶片的光抑制和长出新的阴生叶,通过取得生长优势来增强光合作用。台风还可以产生微环境异质性,使各种生态特征的物种能够共存。灾难性强风干扰过后,由于林冠疏开引起光照增强,以往受抑制的下层植被的快速生长[70]。台风过后藤本植物、草本植物

生长[71-72],落叶植物重新长出新叶,随后树木新枝条和茎杆大量萌芽并生长[8,30]。

台风袭击过程中或刚袭击过后,森林以树木死亡为主。在台风破坏后的几年中,郁闭的林冠层的疏开促进了先锋树种的大量增加、生长和成熟[73],形成的林隙也为个体更新提供了生长机会[74],苗木的更新和植被恢复逐渐占据主导地位,台风前生长非常缓慢的树木也加快直径生长[75],林冠下出现的一些新幼苗能成为新的先锋幼树[76]。另外,强风造成了土壤基质的多样化,从而促进了实生苗和幼树的更新。由于强阳性植物的迅速恢复以及罕见物种的多度增加,多样性持续增加。台风过后的温带森林产生一些林窗斑块,光和土壤养分等资源在这些林窗斑块中重新配置,物种多样性在镶嵌性复合斑块范围内会有所增加。新物种可能侵入这些资源竞争减弱的环境,导致物种多样性增加[77]。

台风后树木产生了新的再生机制[41,78]。在遭受过强风的温带森林中,林木产生大量萌条[74,79]。树木发芽在受到严重干扰的初始演替阶段起到了直接更替的作用。一些没有明显受到破坏的树木在台风干扰后长出独立的芽,从而延长其寿命。二次发芽作为一种重新生长的策略,可以用来弥补因种子减少带来的生长问题。对于经常有台风的地点,树木一般采取多次发芽来抵御这种损害。因此,那些有树干残体的树木更容易以发芽的形式去恢复它们受损的生物量,甚至一些没有受到破坏的树木也会发芽。美国温带的皮德蒙特高原森林受到灾难性强风袭击后,幼苗密度和物种丰度急剧下降,随后幼苗的密度快速回升,植物的丰富度和多样性也逐渐恢复[38-39]。

台风发生时,引起林冠层树种的机械损害或死亡,改变了物种组成及种群的空间分布格局,引起物种多样性发生变化[14,56,74]。台风引起雨水和温度的改变,带来促进土壤种子库中休眠种子的萌发,或导致一些幼苗或种子被冲刷走,短时间内种群的个体数量迅速减少[80]。短期内物种多样性在乔木层中下降,而在幼树层和草本层中上升[4]。林冠层树种的毁坏,减弱了对下层林木的竞争,林窗的形成引起重新配置诸如光、土壤养分等有限的资源,加快入侵物种进入自然森林[81-82],所以物种多样性随着群落的恢复而逐渐增加[76,83]。台风干扰后先锋树种首先出现,接着在短期内消失,较为耐阴植物取代其位置[35]。台风导致植物优势种类减少,而稀有种类出现,使植物种类的分布更加均匀[84]。例如,Horvitz 等发现,美国南佛罗里达州的台风过后不久,植物种类增加了 28%,其中包括 34% 的藤本植物和 24% 的其他物种。非乡土物种的盖度或频度普遍超越乡土树种。台风过后 2 a,乡土和非乡土物种的密度增加。乡土树种往往比非乡土物种更容易萌芽,表现出更强的再生更新能力[81]。Peet 等发现 Hazel 台风在美国北卡罗来纳州皮德蒙特地区发生 23 a 后,落叶阔叶林的植物种丰富度显著增加[85]。群落演替早期由于林窗引起环境多样性使植物种类增加,但森林的自然稀疏可再次导致植物种类多样性的降低[86]。此外,台风也通过改变栖息地结构来影响物种丰富度,例如粗木质残体,枯枝落叶层,地洞和土墩[87-88],以及繁殖可用性[89]都可以影响物种多样性。但是,受到台风严重干扰的森林系统可能导致过量的阳光辐射和干燥的土壤,对喜欢阴暗潮湿环境的物种产生负面影响,其物种丰富度低于原来的森林[90]。

从台风对生物多样性的长期影响来看,在热带森林地区和台风频繁的沿海温带地区,强大的台风对生物多样性的影响相对较小,而对温带森林生物种多样性的影响显著,引起植物数量和一些植物种的再生能力显著增加[91]。

3　台风对森林土壤的影响

台风导致的凋落物输入量与森林特征,包括树木种类、结构、树木叶片量和空间位置相关。台风带来了大量降雨,引起的地表径流冲走了森林内部分原有的枯枝落叶和土壤,使植株分布在土壤表面的根系暴露[18],因而局地受灾的森林内凋落物总量常低于正常凋落物量。另一方面,台风大幅度增加了受灾森林的粗死木质残体(风倒木、风折木、被压木以及树木残根等)和非生理性凋落物的数量,影响生态系统过程。台风引起凋落物和养分输入量的增加。1991 年波多黎各的台风引起凋落物输入量达为 1006—1083 g/m^2,凋落叶中氮和磷的输入量分别正常凋落物为 13 和 1.5—2.4 倍[92]。波多黎各比斯利流域的卢基约试验林中,通过凋落物转移到林地的氮、磷和钾的比例分别达 20%、17% 和 13%[93]。受台风影响的森林年凋落物量下降,在

台风过后3个月才能逐步增加[7]。大量非生理性的枯枝落叶可能影响光合作用,进而影响次年生态系统初级生产力,也显著影响到森林的碳循环、土壤养分在时间和空间上的分配、植物幼苗生长和更新、动物群落的生存、土壤微生物和腐食性小动物的生境[63],最终影响植被和动物群落的演替。这些凋落物在台风后将逐步通过土壤微生物和腐食性小动物等的分解归还到土壤、水体和大气中。台风产生的凋落物的养分含量比正常凋落物高,原因是其没有经历正常凋落前的养分回流阶段,因此分解速率快,能较快释放营养元素,加快循环。

台风造成的树木连根拔起、树干折断、树冠受损和叶片脱落,可以使森林生态系统地上活生物量碳转化为死亡木和凋落物碳。树木重新长出新叶后,凋落物量才有可能增加,这会影响到台风后几个月内的林地碳和养分持续输入[7]。年幼个体比成熟林木的净初级生产力速率高,因此热带风暴过后,森林可能会有更大的碳截获能力。台风产生的粗死木和枯枝落叶使森林的碳储量迅速归还土壤[82],这是森林碳循环过程中碳库的重要来源之一[94-95]。碳的快速归还导致碳循环过程明显加快,碳储量在森林环境的不同空间得到重新分配。短期内迅速回归的碳中仅有15%返回到森林中,剩下的大部分被分解后释放,最终回到大气中[95]。

台风产生的粗死木质残体和凋落物为其它动物提供生长的生境,维持森林结构的多样性,补充了林地养分。在地势比较复杂的丘陵山地,台风引起的地表径流往往导致土壤中的养分流失。由于台风干扰而造成某些高于正常养分含量的凋落物突然的大量输入能影响养分循环,特别是氮和磷循环[96]。台风造成的叶凋落物中氮浓度为正常叶凋落物的1.30—1.38倍,磷为1.92—2.28倍,K为1.74—1.91倍[97]。台风干扰造成的凋落物(尤其是绿色的嫩叶)分解速率比正常落叶更快,磷和氮的循环加快,土壤中的磷和氮的有效性增加[98]。所以从鲜叶分解的养分释放率可能超过植被、微生物和土壤在生态系统保有养分的能力[99]。因此,养分容易淋失(特别是在强降雨条件下)。

台风对养分循环有重要影响。台风期间和之后溪水中的氮、磷和钾的浓度显著升高。开始这种效应是由于土壤水分冲洗出来,并且土壤水分中有大量的离子。从长远来看由台风干扰增加了土壤中养分流失,会增加分解和减少养分吸收[93]。在海南岛台风引起暴雨发生后,N、Mg、Ca、K的输入大于输出,P、Al、Si的输入小于输出[99]。波多黎各一处水源涵养林台风后的地表径流导致矿质元素的损失,土壤中K的流失量和N的气化损失量增加,NH_4和NO_3的流失量也略有增加[100]。

4 台风对动物的影响

台风通过折断树枝,连根拔起树木[101],以及脱落叶片和果实等方式来毁灭植物[102-103],减少动物的食物供应[102-104]和恶化栖息地的环境[105]。Labisky等[106]发现,台风引起的落叶和泥浆能覆盖和隐藏食物,减少白尾鹿(*Odocoileus virginianus*)的食物供应,导致其受精率降低和后代存活率降低。

台风过境可以杀死暴露于风雨的鸟类[107]。例如,台风8个月后美属维尔京群岛的鸟数量比台风前显著降低[108]。经历台风幸存下来的鸟类是虚弱的,容易受到捕食或者死亡率增加。摄食习性似乎对山地森林鸟类的减少作用最大,食蜜类和食果实/种子的鸟类减少的程度要比食虫类和猛禽类高得多。随着林窗引起的森林郁闭度降低和大量枝叶残体转移到森林地面,动物的生活条件发生重大变化。台风改变了以往在不同林冠层中觅食分层的正常秩序[109],处于林冠的鸟类被迫到森林地面或林下叶层觅食[110]。台风可以引起单株倒木或大规模的倒树,从而产生多种尺寸的林窗[111-112]。单株倒木可以为一些地面筑巢鸟类创造一个很好的筑巢地点,却使一些生活在林冠层的节肢动物的栖息地退化;由许多倒木造成的林窗可以作为一些草原鸟丰富的觅食斑块或者作为一些草原节肢动物理想的栖息地斑块。

台风对昆虫有明显的影响[113]。台风携带昆虫并使昆虫分散很远地方[114]。成熟或半成熟的森林损害给害虫滋生提供了场所[115]。台风通过对食物来源或者捕食者的作用影响昆虫种群数量,能导致当地物种灭绝或大规模爆发[113]。例如台风雨果袭击后,鳞翅目中15个物种种群数量爆发增长,其中甜菜夜蛾出现在56种植物上。

5 展望

尽管目前已经有很多台风对森林损伤和森林在林隙动态和演替方面短期效应的研究,但是对于在台风干

扰条件下的森林恢复、优势幼树和新生幼苗之间竞争的长期效应研究较少。开展受台风干扰的森林组成、植物多样性和演替的长期监测,对于认识台风的长期影响是十分重要的。

全球气候变化是人类共同面临的难题。气候变暖引起极端气候灾害增多,台风频繁。森林生态系统在减缓大气 CO_2 等温室气体浓度上升以及维护全球碳平衡方面起着极其重要的作用。台风导致森林叶片的剧减,影响植物光合作用,产生的大量的粗死木质残体和凋落物增加了林地的有机碳贮量,而台风带来的降水可能会影响土壤动物和土壤微生物的活动,进而改变土壤呼吸,导致森林土壤有机碳库释放 CO_2 的速度发生变化,从而影响森林土壤有机碳的贮藏及土壤碳动态。目前关于台风对森林生态系统生物量变化和碳循环的研究十分薄弱,探索不同森林土壤有机碳贮藏对台风的响应是研究森林对气候变化的适应和响应机制的重要组成部分。

台风带来的暴雨往往会造成森林生态系统的地表径流和泥石流,引起土壤养分的流失。然而目前缺乏对台风侵袭时森林土壤和养分流失的研究。开展台风过程中不同森林土壤和养分流失规律的研究,对进一步认识森林的水文生态功能有重要的意义。

台风产生大量积聚于地表的粗死木质残体和凋落物,在高温干燥的条件下容易诱发森林大火。另外,大量的林冠受损为害虫爆发和真菌感染提供了条件,可能增加森林的受害程度。因此森林受台风和其他自然灾害的交叉影响的研究是目前国际上研究的热点之一。

建立数学模型和采用计算机模拟方法可以评估台风损害和预测森林对台风的响应。目前在构建此类模型方面已取得一些进展,但是现有模型的应用局限于一定地域的某些森林类型。因此需要改进有关模型的参数,使之能预测台风对不同森林类型的影响。应用遥感技术和地理信息系统技术结合受台风影响森林的资料,建立大尺度台风损害森林过程的模型,将使这些模型成为灾后森林恢复的有效工具。

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ACTA ECOLOGICA SINICA Vol. 32, No. 5 March, 2012 (Semimonthly)

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国内邮发代号:82-7　国外邮发代号:M670　标准刊号:ISSN 1000-0933　CN 11-2031/Q

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生　态　学　报
(SHENGTAI　XUEBAO)
(半月刊　1981 年 3 月创刊)
第 32 卷　第 5 期　(2012 年 3 月)

ACTA ECOLOGICA SINICA
(Semimonthly, Started in 1981)
Vol. 32　No. 5　2012

编　　辑	《生态学报》编辑部 地址:北京海淀区双清路 18 号 邮政编码:100085 电话:(010)62941099 www. ecologica. cn shengtaixuebao@ rcees. ac. cn
主　　编	冯宗炜
主　　管	中国科学技术协会
主　　办	中国生态学学会 中国科学院生态环境研究中心 地址:北京海淀区双清路 18 号 邮政编码:100085
出　　版	科学出版社 地址:北京东黄城根北街 16 号 邮政编码:1R00717
印　　刷	北京北林印刷厂
发　　行	科学出版社 地址:东黄城根北街 16 号 邮政编码:100717 电话:(010)64034563 E-mail:journal@ cspg. net
订　　购	全国各地邮局
国外发行	中国国际图书贸易总公司 地址:北京 399 信箱 邮政编码:100044
广告经营许可证	京海工商广字第 8013 号

Edited	by	Editorial board of ACTA ECOLOGICA SINICA Add:18, Shuangqing Street, Haidian, Beijing 100085, China Tel:(010)62941099 www. ecologica. cn Shengtaixuebao@ rcees. ac. cn
Editor-in-chief		FENG Zong-Wei
Supervised	by	China Association for Science and Technology
Sponsored	by	Ecological Society of China Research Center for Eco-environmental Sciences, CAS Add:18, Shuangqing Street, Haidian, Beijing 100085, China
Published	by	Science Press Add:16 Donghuangchenggen North Street, Beijing 100717, China
Printed	by	Beijing Bei Lin Printing House, Beijing 100083, China
Distributed	by	Science Press Add:16 Donghuangchenggen North Street, Beijing 100717, China Tel:(010)64034563 E-mail:journal@ cspg. net
Domestic		All Local Post Offices in China
Foreign		China International Book Trading Corporation Add:P. O. Box 399 Beijing 100044, China

ISSN 1000-0933　CN 11-2031/Q　国内外公开发行　国内邮发代号 82-7　国外发行代号 M670　定价 70.00 元