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生态学报

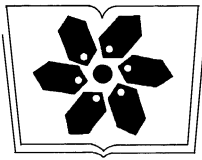
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目 次

基于景观格局理论和理想风水模式的藏族乡土聚落景观空间解析——以甘肃省迭部县扎尕那村落为例·····	史利莎,严力蛟,黄璐,等 (6305)
武夷山风景名胜区景观生态安全度时空分异规律·····	游巍斌,何东进,巫丽芸,等 (6317)
旅游地道路生态持续性评价——以云南省玉龙县为例·····	蒋依依 (6328)
城市空间形态紧凑度模型构建方法研究·····	赵景柱,宋瑜,石龙宇,等 (6338)
丹顶鹤多尺度生境选择机制——以黄河三角洲自然保护区为例·····	曹铭昌,刘高焕,徐海根 (6344)
西南喀斯特区域水土流失敏感性评价及其空间分异特征·····	凡非得,王克林,熊鹰,等 (6353)
流域尺度海量生态环境数据建库关键技术——以塔里木河流域为例·····	高凡,闫正龙,黄强 (6363)
雌雄异株植物鼠李的生殖分配·····	王娟,张春雨,赵秀海,等 (6371)
长白山北坡不同年龄红松年表及其对气候的响应·····	王晓明,赵秀海,高露双,等 (6378)
不同高寒退化草地阿尔泰针茅种群的小尺度点格局·····	赵成章,任珩,盛亚萍,等 (6388)
残存银杏群落的结构及种群更新特征·····	杨永川,穆建平, TANG Cindy Q, 等 (6396)
濒危植物安徽羽叶报春两种花型的繁育特性及其适应进化·····	邵剑文,张文娟,张小平 (6410)
神农架海拔梯度上 4 种典型森林的乔木叶片功能性状特征·····	罗璐,申国珍,谢宗强,等 (6420)
不同植被恢复模式下煤矸石山复垦土壤性质及煤矸石风化物的变化特征·····	王丽艳,韩有志,张成梁,等 (6429)
火烧对黔中喀斯特山地马尾松林分的影响·····	张喜,崔迎春,朱军,等 (6442)
内蒙古高原锦鸡儿属植物的形态和生理生态适应性·····	马成仓,高玉葆,李清芳,等 (6451)
古尔班通古特沙漠西部梭梭种群退化原因的对比分析·····	司朗明,刘彤,刘斌,等 (6460)
白石砬子国家级自然保护区天然林的自然稀疏·····	周永斌,殷有,殷鸣放,等 (6469)
黑龙江省东完达山地区东北虎猎物种群现状及动态趋势·····	张常智,张明海 (6481)
基于 GIS 的马铃薯甲虫扩散与河流关系研究——以新疆沙湾县为例·····	李超,张智,郭文超,等 (6488)
2010 年广西兴安地区稻纵卷叶螟发生动态及迁飞轨迹分析·····	蒋春先,齐会会,孙明阳,等 (6495)
B 型烟粉虱对寄主转换的适应性·····	周福才,李传明,顾爱祥,等 (6505)
利用 PCR-DGGE 方法分析不同鸡群的盲肠微生物菌群结构变化·····	李永洙, Yongquan Cui (6513)
鸡粪改良铜尾矿对 3 种豆科植物生长及基质微生物量和酶活性的影响·····	张宏,沈章军,阳贵德,等 (6522)
铜绿微囊藻对紫外辐射的生理代谢响应·····	汪燕,李珊珊,李建宏,等 (6532)
10 种常见甲藻细胞体积与细胞碳、氮含量的关系·····	王燕,李瑞香,董双林,等 (6540)
冬季太湖表层底泥产毒蓝藻群落结构和种群丰度·····	李大命,孔繁翔,于洋,等 (6551)
城市机动车道颗粒物扩散对绿化隔离带空间结构的响应·····	蔺银鼎,武小刚,郝兴宇,等 (6561)
新疆城镇化与土地资源产出效益的空间分异及其协调性·····	杨宇,刘毅,董雯,等 (6568)
山东潍坊地下水硝酸盐污染现状及 $\delta^{15}\text{N}$ 溯源·····	徐春英,李玉中,李巧珍,等 (6579)
增温对宁夏引黄灌区春小麦生产的影响·····	肖国举,张强,张峰举,等 (6588)
一种估测小麦冠层氮含量的新高光谱指数·····	梁亮,杨敏华,邓凯东,等 (6594)
黄河上游灌区稻田 N_2O 排放特征·····	张惠,杨正礼,罗良国,等 (6606)
专论与综述	
植物源挥发性有机物对氮沉降响应研究展望·····	黄娟,莫江明,孔国辉,等 (6616)
植物种群更新限制——从种子生产到幼树建成·····	李宁,白冰,鲁长虎 (6624)
研究简报	
遮荫对两个基因型玉米叶片解剖结构及光合特性的影响·····	杜成凤,李潮海,刘天学,等 (6633)
学术信息与动态	
科学、系统与可持续性——第六届工业生态学国际大会述评·····	石海佳,梁赛,王震,等 (6641)
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封面图说: 鹤立——丹顶鹤是世界 15 种鹤数量极小的一种,主要栖息在沼泽、浅滩、芦苇塘等湿地,以捕食小鱼虾、昆虫、蛙蚺、软体动物为主,也吃植物的根茎、种子、嫩芽。善于奔驰飞翔,喜欢结群生活。丹顶鹤属迁徙鸟类,主要在我国的黑龙江、吉林、俄罗斯西伯利亚东部、朝鲜北部以及日本等地繁殖。在长江下游一带越冬。在中国文化中有“仙鹤”之说。被列为中国国家一级重点保护野生动物名录,濒危野生动植物种国际贸易公约绝对保护的 CITES 附录一物种名录。

彩图提供: 陈建伟教授 国家林业局 E-mail: cites.chenjw@163.com

周永斌, 殷有, 殷鸣放, 张飞. 白石砬子国家级自然保护区天然林的自然稀疏. 生态学报, 2011, 31(21): 6469-6480.

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白石砬子国家级自然保护区天然林的自然稀疏

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摘要:以白石砬子自然保护区 14 个天然林为研究对象,利用近 30 a 间 14 次的连续定位观测数据,分析了各林分自然稀疏过程中 Reineke 方程指数 β 值的变化范围,阐明了 β 值恒定的机制与影响因素。结果表明,白石砬子自然保护区天然林随着林分密度的降低,林分平均胸径逐年提高;14 个天然林中,平均胸径与林分密度的幂函数相关性均达到极显著水平,其中 9 个天然林的幂指数 β 值约为 1.5;5 个天然林 β 值变化范围较大,在 0.44—1.80 之间。对 β 值波动的 5 个林分进一步分析,1、9、56 号林分受到明显的人为干扰;22、23 号林分分别在林分密度较大和胸径生长量较高的时间范围内, β 值约为 1.5。在天然林的自然稀疏过程中,枯损林木呈左偏单峰状分布,大径阶木死亡数量较低,中小径阶的被压木死亡数量较大,形成了树木间的负反馈关系。综合本研究表明,白石砬子自然保护区天然林的自然稀疏是连续的过程,符合 $-3/2$ 自疏法则, β 值恒定,约为 $3/2$;而 β 值是否恒定,与立地、树种组成等因素无关,与人为干扰有关;林木之间的负反馈机制是发生自然稀疏的根本原因,光是影响自然稀疏的主要因子。

关键词:天然林; $-3/2$ 自疏法则;密度调控机制;负反馈

Self-thinning of natural broadleaved forests in Baishilazi Nature Reserve

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Abstract: Self-thinning is a hot issue in ecological theoretical research and has important practical significance in terms of guiding forestry production. Adoption of dynamic data on the number of trees in a stand and the size of the stand in investigating self-thinning is the key to establishing stand density theory. Taking data from 14 investigations on 14 natural broad-leaved stands in Baishilazi Nature Reserve in Northeast China over the past 30 years, this paper provides evidence for establishing a theory of stand density control. This paper analyzes the variation range for parameter β within the empirical equation $N = kD^{-\beta}$ described by Reineke, where N is the stand density and D is the average diameter at breast height (DBH), and explains factors that may make β constant. Results show that with a reduction in stand density, the DBH of a stand increases year by year. Moreover, among the 14 natural broad-leaved communities studied, the power functions of the DBH and stand density both become significant; the exponent β for the No. 17, 33, 35, 38, 49, 50, 61, 67, and 68 natural broadleaved communities is about 1.5, and the variation in β for the No. 1, 9, 22, 23, and 56 natural broadleaved communities is 0.44—1.80. Through further analysis of the fluctuation in β for the five latter stands, it is clear that No. 1, 9, and 56 stands are disturbed by obvious human activities. The number of dead plants in stand No. 22 was 387.5 per hectare in the 15 years from 1993 to 2008 but only 200 in the 12 years from 1979 to 1991, an increase of a factor of 1.94. Therefore, this paper chooses data from 1993 to 2008 for simulation, for which β is 1.57. The average DBH of stand No. 23 increased only 1.95 cm in the 13 years from 1993 to 2008 but 3.72 cm in the 16 years from 1979 to 1993. Thus, this paper adopts data for the 16 years from 1979 to 1993 for simulation, for which β is 1.59. In the self-thinning process, the

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distribution of tree mortality can be fitted to a unimodal function with a peak skewed to smaller trees, resulting in low mortality for trees with large diameter and high mortality for suppressed trees with small and medium diameters. Meanwhile, a negative feedback relationship forms between the upper- and lower-layer trees. Overall, our results indicate that self-thinning in natural broadleaved forests is a continuous process that is in accordance with a $-3/2$ power law. The power index β found in this study is constant—with a value of $-3/2$ —and correlates with human disturbance rather than the forest site, species composition, and other factors. Self-thinning in natural forests is the consequence of the negative feedback relationship noted above and is controlled primarily by light intensity. Self-thinning in natural broad-leaved forests is in line with the $-3/2$ power law, which shows that forest ecosystems of the nature reserve are strongly self-regulating and have a certain stability. Therefore, the avoidance of human disturbance whenever possible, and the maintaining and ensuring of the stability and sustainability of forest ecosystems are necessary in forest ecosystem management.

Key Words: natural broad-leaved community; $-3/2$ power law of self-thinning; density control; negative feedback

在个体密度非常高的植物群落中,随着群落的生长而个体密度逐渐降低的现象,称为自然稀疏。它是群落所具有的自我调节机能之一,通过密度调控把个体适应、种群数量动态、生物群落演替与生态系统稳定性联系起来,一直是生态学领域研究的热点问题^[1-4],对指导林业生产具有重要的实践意义^[5-10]。 $-3/2$ 法则表达了在密度调控下植物大小与种群密度的关系^[6,11],表达式为: $W = kN^{-\alpha}$, 其中平均生物量, N 为株数密度, k 、 α 为参数,其中 α 值接近 $-3/2$,该模型被定义为“自然稀疏法则”^[12]。许多学者用植株平均大小与几何形状、异速生长之间的关系来推导与论证这一法则^[6,13-22]。 $-3/2$ 法则被公认为与植物生长的几何形状有关^[23-24]。基于异速生长规律的 $-4/3$ 自疏规律是不同于 $-3/2$ 法则的另一理论,揭示了生物个体新陈代谢率与身体大小之间的关系,描述表达式为: $B \propto M^{-3/4}$, 其中 B 为个体的新陈代谢率, M 为个体的大小^[15,25]。在自然稀疏规律的影响因素研究中,光、水、养分和温度等非生物因素能直接影响群落的自然稀疏指数^[26-29],也有研究表明,基因、激素等细胞内因素对自然稀疏指数产生间接的影响^[30-32]。

由于森林的生长周期长,自然稀疏过程具有长期性、复杂性、非线性等特征,无论是 $-3/2$ 法则还是 $-4/3$ 自疏规律,在森林自然稀疏规律研究中均无法获得一致的认可^[22,25,33-36],其中,采用以空间代替时间的方法,把互不相干的林分数据罗列在一起进行静态统计分析的研究方法,是自然稀疏规律研究中产生争议与分歧的主要原因之一^[37-38]。因而,近几年研究者们开始尝试用动态的个体植物之间的竞争来建立模型^[18-19],采用同一林分的林木大小与株数之间动态数据研究自然稀疏规律,是建立林分密度理论的关键^[39-40]。

白石砬子国家级保护区位于辽宁省宽甸县境内,是东北亚地区天然次生林植被保存最完好的区域。白石砬子自然保护区建立后,采用系统布点方式在全区设置 68 块固定标准地,对胸径大于 5.0 cm 的树木逐株编号,从 1979 年起至今,每隔 2 a 进行一次系统的定位调查,至 2008 年已连续调查 14 次。本文利用白石砬子自然保护区近 30 a 间累计的连续观测资料,对天然林的林木密度与胸径动态变化规律进行研究,以为林分自然稀疏理论研究提供证据,为全球气候变化条件下自然保护区森林生态系统管理提供依据。

1 研究区域概况

1.1 自然概况

白石砬子自然保护区位于辽宁省东南部宽甸县,地处 $124^{\circ}44'07''$ — $124^{\circ}57'30''$ E, $40^{\circ}50'00''$ — $40^{\circ}57'127''$ N,总面积为 7405 km^2 。属于长白山余脉千山山系,海拔高度一般为 400—1200 m,是典型的中山地带。保护区是我国东北地区的暴雨中心,年平均降水量 1600 mm,最高降水量达 2186.7 mm。全区相对湿度平均为 73%。雨热同季,均为 7—9 月。

1.2 数据来源

课题组参加了 2008 年的白石砬子自然保护区标准地调查,2008 年以前的 13 次调查数据由自然保护区提供。数据包括 14 个天然林的标准地概况、编号树木的种名与胸径。

由表1可见,各林分树种组成比例均未超过3成,其中蒙古栎(*Quercus mongolica*)、紫椴(*Tilia amurensis*)、假色槭(*Acer pseudo-sieboldianum*)、色木槭(*Acer mono*)、赛黑桦(*Betula schmidtii*)居多,混生少量的树种有花曲柳(*Fraxinus rhynchophylla*)、山杨(*Populus davidiana*)、裂叶榆(*Ulmus laciniata*)、花楸(*Sorbus pohuashanensis*)、花楷槭(*Acer ukurunduense*)、千金榆(*Carpinus cordata*)、暴马丁香(*Syringa amurensis*)、怀槐(*Maackia amurensis*)、核桃楸(*Juglans mandshurica*)、黄波罗(*Phellodendron amurense*)、斑叶稠李(*Prunus maackii*)、灯台树(*Cornus controversa*)、山樱桃(*Prunus verecunda*)、红松(*Pinus koraiensis*)、臭冷杉(*Abies nephrolepis*)、鱼鳞云杉(*Picea jazoensis*),共21种。

表1 白石砬子自然保护区天然林标准地基本信息

Table 1 Basic information of natural broad-leaved community sample plot in the Baishilazi Natural Reserve

序号 No.	标准地号 No. of sample-plot	海拔高度 Altitude/m	坡向 Slope direction	最优树种 Percent of optimal tree species	比例/%
1	1	377	WN	蒙古栎 <i>Qrercus mongolica</i>	29
2	9	780	WN	假色槭 <i>Acer pseudo-sieboldianum</i>	29
3	17	866	W	紫椴 <i>Tilia amurensis</i>	27
4	22	700	WN	假色槭 <i>Acer pseudo-sieboldianum</i>	23
5	23	860	W	色木槭 <i>Acer mono</i>	0.29
6	33	990	WN	假色槭 <i>Acer pseudo-sieboldianum</i>	24
7	35	978	E	假色槭 <i>Acer pseudo-sieboldianum</i>	28
8	38	750	WN	花楷槭 <i>Acer ukurunduense</i>	17
9	49	800	ES	千金榆 <i>Carpinus cordata</i>	22
10	50	1068	E	色木槭 <i>Acer mono</i>	26
11	56	630	WN	赛黑桦 <i>Betula schmidtii</i>	29
12	61	800	E	色木槭 <i>Acer mono</i>	27
13	67	940	S	色木槭 <i>Acer mono</i>	28
14	68	700	WN	紫椴 <i>Tilia amurensis</i>	26

1.3 数据处理

林分密度与胸径动态以平均值±标准差形式给出。

选择 Reineke 提出的幂函数方程对自然稀疏规律进行模拟: $N = kD^{-\beta}$, 其中 N 为林分密度 (N/hm^2), D 为平均胸径 (cm), k, β 为常数。

按 2 cm 整化径阶, 统计每间隔 10 a 各径阶实际林木枯损株数, 分析天然林自然稀疏总的趋势与调控机制。

2 结果与分析

2.1 天然林林分结构动态及幂函数模拟曲线

通过图 1a—图 14a 可以看出, 白石砬子自然保护区天然林自然稀疏现象明显, 且具有连续性。随着林分密度的降低, 林分平均胸径逐年提高。

通过图 1b—图 14b 可以看出, 林分密度与胸径之间具有显著的相关性, 14 个林分中有 9 个林分的幂指数约为 3/2, 5 个林分的幂指数与 3/2 差异较大。

2.3 β 值恒定为 3/2 的 9 个林分特征

由表 2 可见, 编号为 17、33、35、38、49、50、61、67、68 的 9 个天然林平均胸径年增长量在 0.13—0.20 cm 之间, 年均死亡 7.67—26.29 N/hm^2 。林分密度和平均胸径的幂函数回归达极显著水平, 幂指数 β 值均均为 1.5。

2.4 β 值不恒定的 5 个林分特征

由表 2 可见, 编号为 1、9、22、23、56 的 5 个天然林平均胸径与林分密度的幂函数相关性均达到极显著水

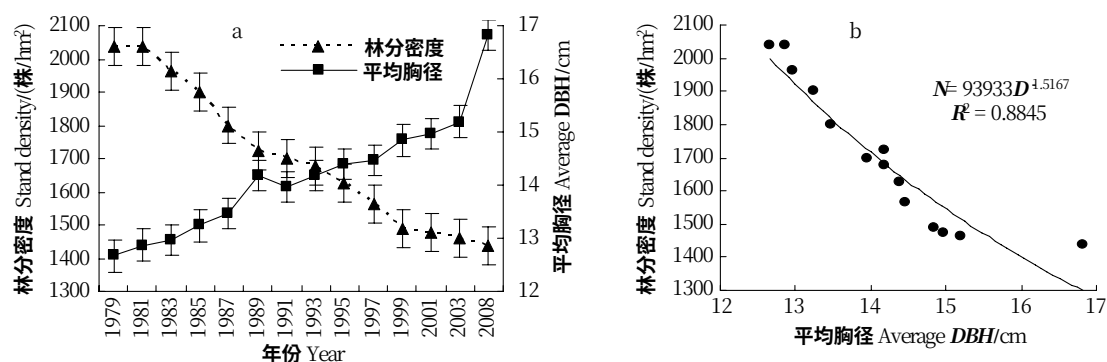


图1 17号标准地林分密度与平均胸径动态及相关关系

Fig. 1 Trend and correlativity of stand density and average DBH for No. 17 sample plot

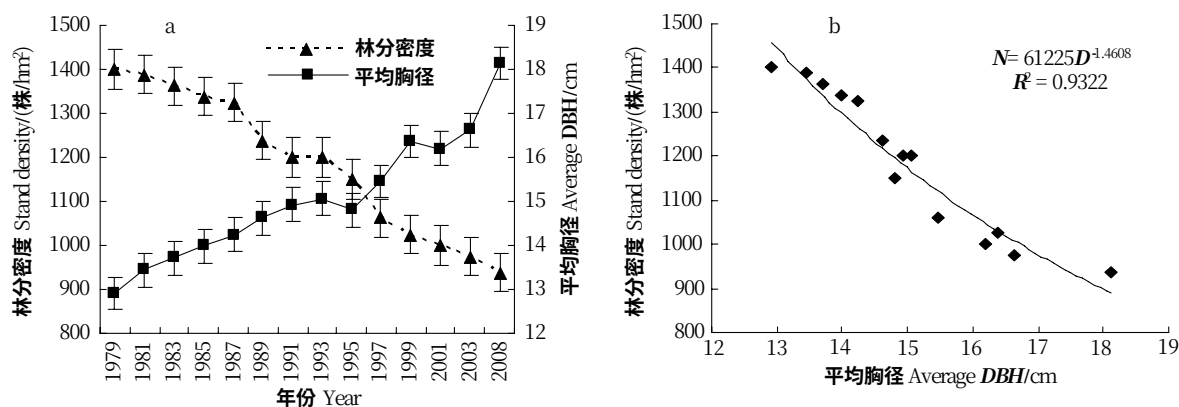


图2 33号标准地林分密度与平均胸径动态及相关关系

Fig. 2 Trend and correlativity of stand density and average DBH for No. 33 sample plot

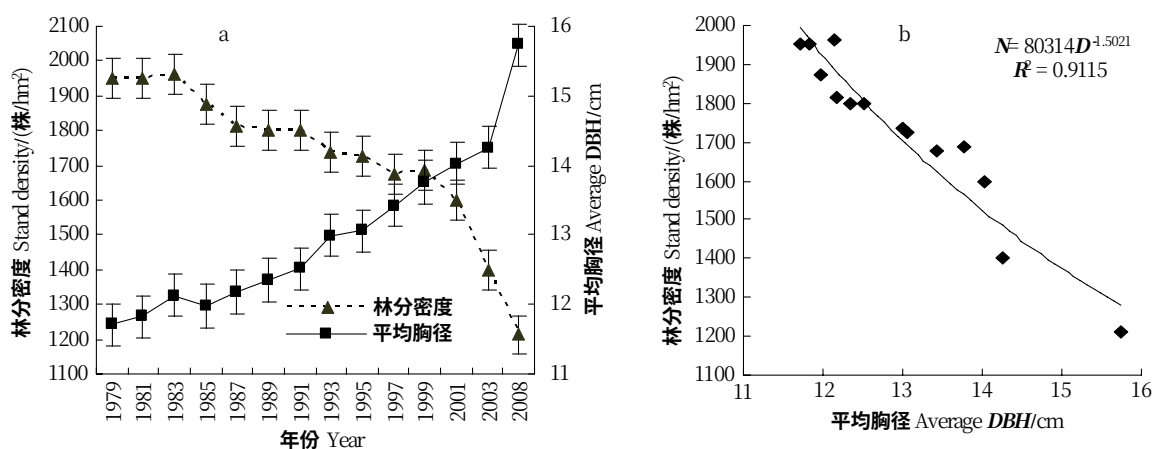


图3 35号标准地林分密度与平均胸径动态及相关关系

Fig. 3 Trend and correlativity of stand density and average DBH for No. 35 sample plot

平,但 β 值变化范围较大,在0.44—1.80之间。

1、9、56号3个林分年均死亡株数较少,约为6 N/hm²。结合图10a、图11a、图14a可见,这3个林分的密度在1985—1993年急剧下降,其余时间变化较小,可能存在人为干扰。与自然保护区管理局沟通后确认,该时间段内自然保护区存在过人为干扰活动。

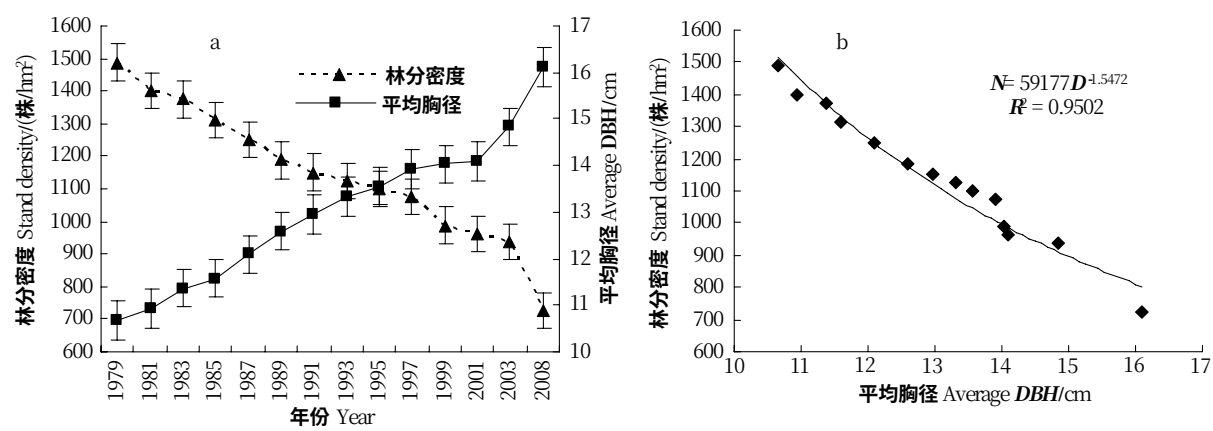


图 4 38 号标准地林分密度与平均胸径动态及相关关系

Fig. 4 Trend and correlativity of stand density and average DBH for No. 38 sample plot

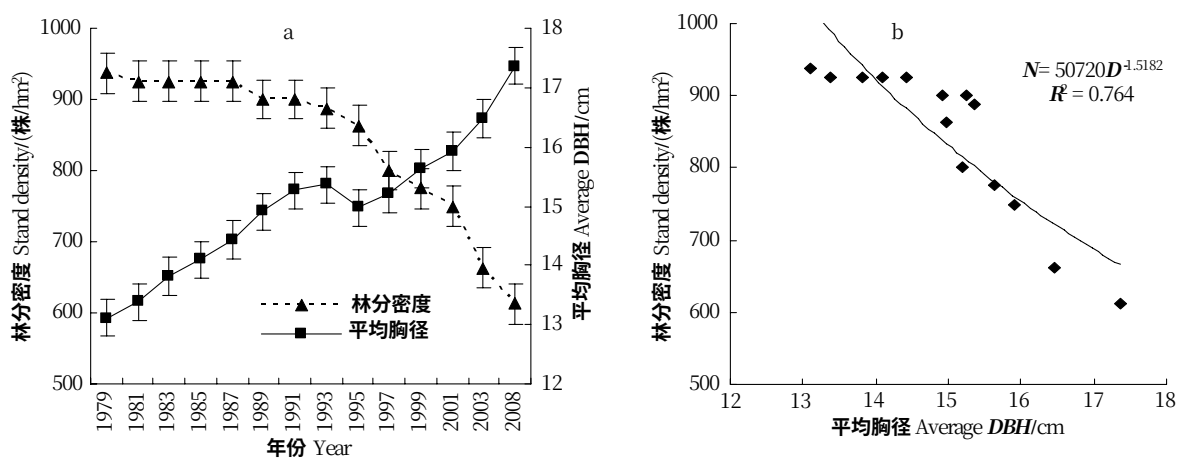


图 5 49 号标准地林分密度与平均胸径动态及相关关系

Fig. 5 Trend and correlativity of stand density and average DBH for No. 49 sample plot

表 2 林分密度、平均胸径变化及相关关系

Table 2 Change and correlativity of stand density and average DBH				
标准地号 No. of sample-plot	平均胸径年增长率 Annual increment of average DBH/(cm/a)	年均死亡株数 Number of annual dead trees /(株/㎡·a ⁻¹)	回归方程 Regression equation	相关系数 Correlation coefficients
17	0.14	20.69	$N = 93933D^{-1.5167}$	$R^2 = 0.8845^{**}$
33	0.18	15.95	$N = 61225D^{-1.4608}$	$R^2 = 0.9322^{**}$
35	0.14	25.43	$N = 80314D^{-1.5021}$	$R^2 = 0.9115^{**}$
38	0.19	26.29	$N = 59177D^{-1.5472}$	$R^2 = 0.9502^{**}$
49	0.15	11.21	$N = 50720D^{-1.5182}$	$R^2 = 0.7640^{**}$
50	0.13	7.67	$N = 46901D^{-1.5418}$	$R^2 = 0.9335^{**}$
61	0.20	21.12	$N = 58947D^{-1.5007}$	$R^2 = 0.9777^{**}$
67	0.21	26.29	$N = 76561D^{-1.5403}$	$R^2 = 0.9921^{**}$
68	0.15	17.24	$N = 63856D^{-1.5081}$	$R^2 = 0.9768^{**}$
1	0.17	6.47	$N = 10096D^{-0.8957}$	$R^2 = 0.9179^{**}$
9	0.23	6.47	$N = 3141.3D^{-0.4405}$	$R^2 = 0.8977^{**}$
22	0.23	21.56	$N = 14549D^{-0.9491}$	$R^2 = 0.9357^{**}$
23	0.20	14.22	$N = 133178D^{-1.8006}$	$R^2 = 0.9863^{**}$
56	0.29	6.03	$N = 7331.8D^{-0.9088}$	$R^2 = 0.9590^{**}$

** $P < 0.01$

22 号林分年均死亡株数较多,结合图 12a 可见,在 1993—2008 年的 15 a 间,则每公顷累计死亡 387.5

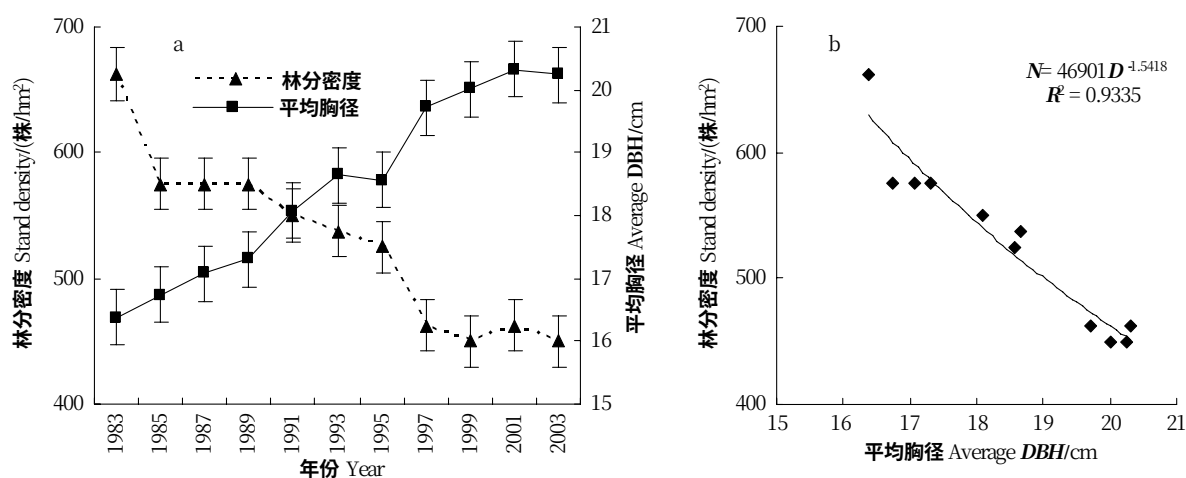


图6 50号标准地林分密度与平均胸径动态及相关关系

Fig. 6 Trend and correlativity of stand density and average DBH for No. 50 sample plot

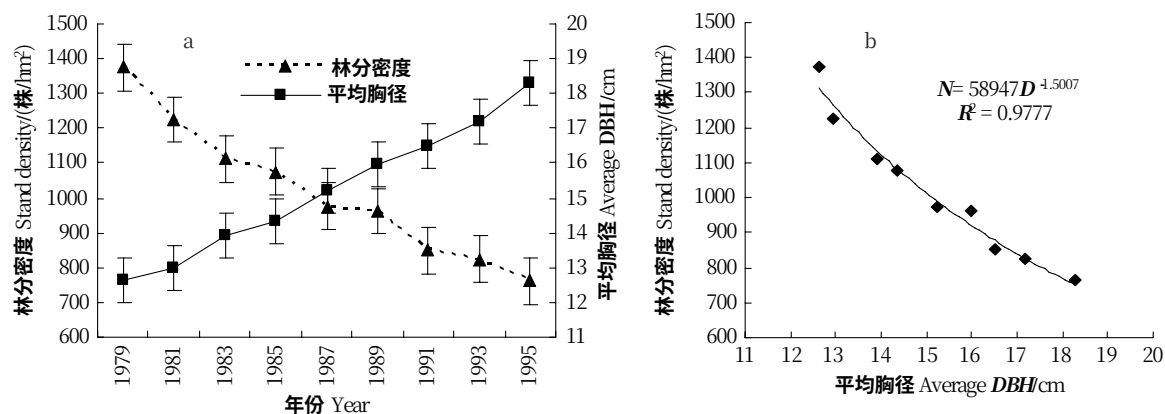


图7 61号标准地林分密度与平均胸径动态及相关关系

Fig. 7 Trend and correlativity of stand density and average DBH for No. 61 sample plot

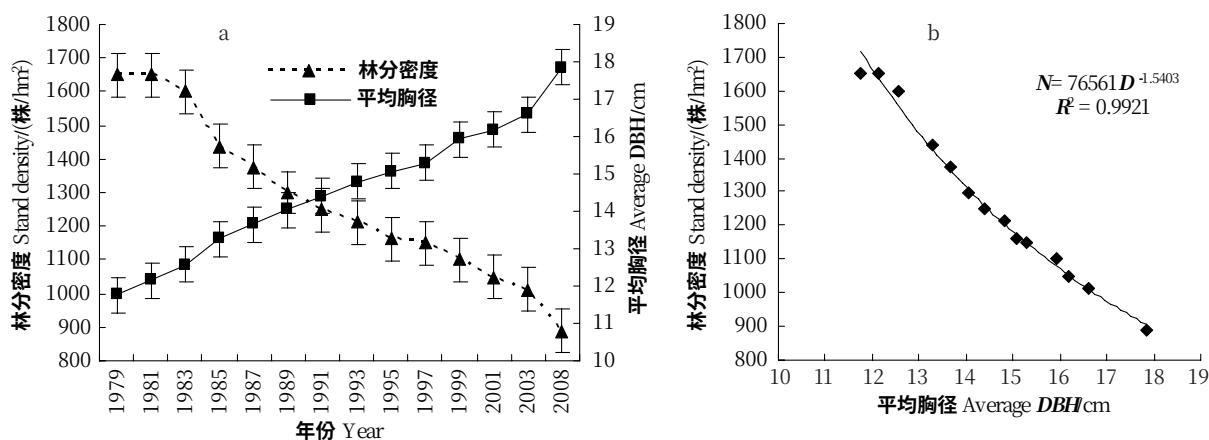


图8 67号标准地林分密度与平均胸径动态及相关关系

Fig. 8 Trend and correlativity of stand density and average DBH for No. 67 sample plot

株;在1979—1991年的12 a间,每公顷累计死亡200株,两个时间段累计死亡株数相差1.94倍。选择用竞争强烈的1993—2008年的数据进行模拟(图15),方程为 $N = 79849D^{-1.5778}$, R^2 为0.9716,相关性显著, β 值约为1.5。

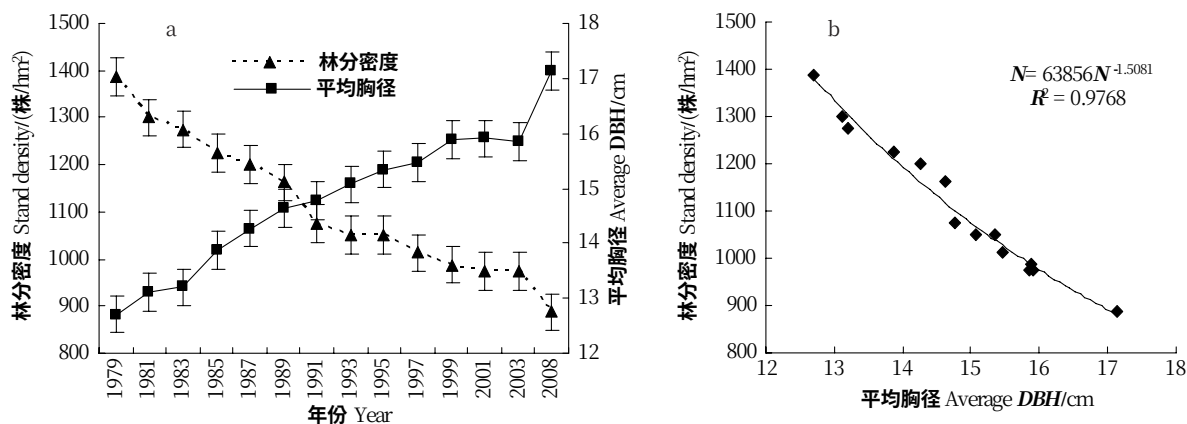


图9 68号标准地林分密度与平均胸径动态及相关关系

Fig. 9 Trend and correlativity of stand density and average DBH for No. 68 sample plot

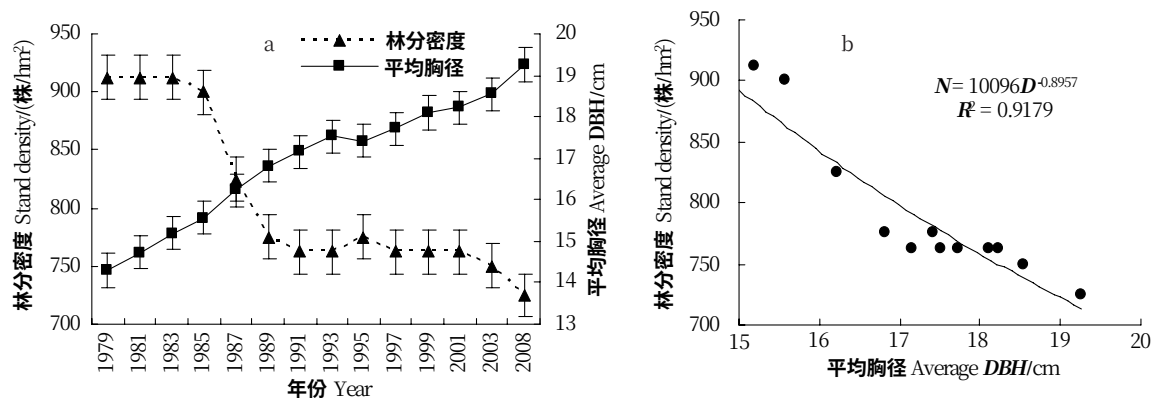


图10 1号标准地林分密度与平均胸径动态及相关关系

Fig. 10 Trend and correlativity of stand density and average DBH for No. 1 sample plot

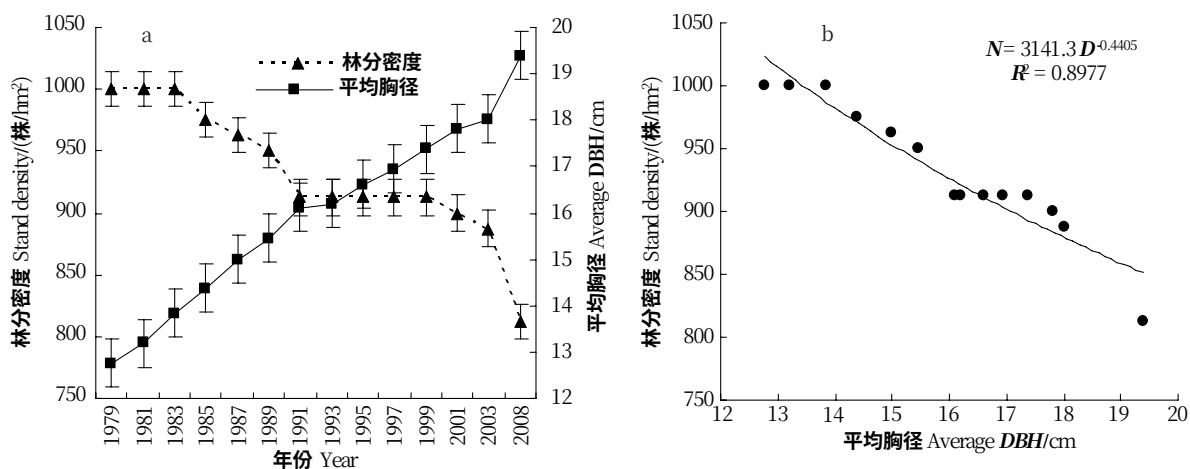


图11 9号标准地林分密度与平均胸径动态及相关关系

Fig. 11 Trend and correlativity of stand density and average DBH for No. 9 sample plot

23号林分平均胸径增长量较小,结合图13a可见,在1979—1993年的14a间,平均胸径增加3.72cm,而后的15a间,仅增长了1.95cm,数据出现异常。因此,对23号标准地,采用1979—1993年的14a间的数据

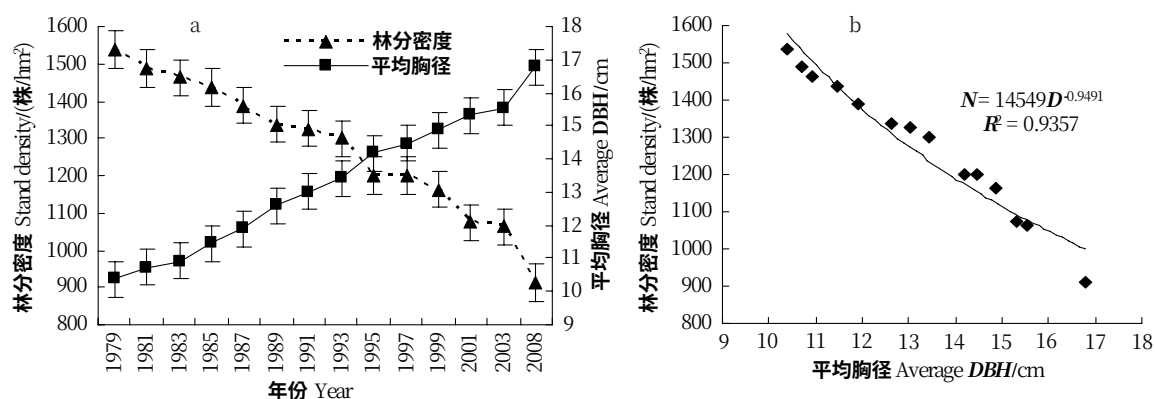


图 12 22 号标准地林分密度与平均胸径动态及相关关系

Fig. 12 Trend and correlativity of stand density and average DBH for No. 22 sample plot

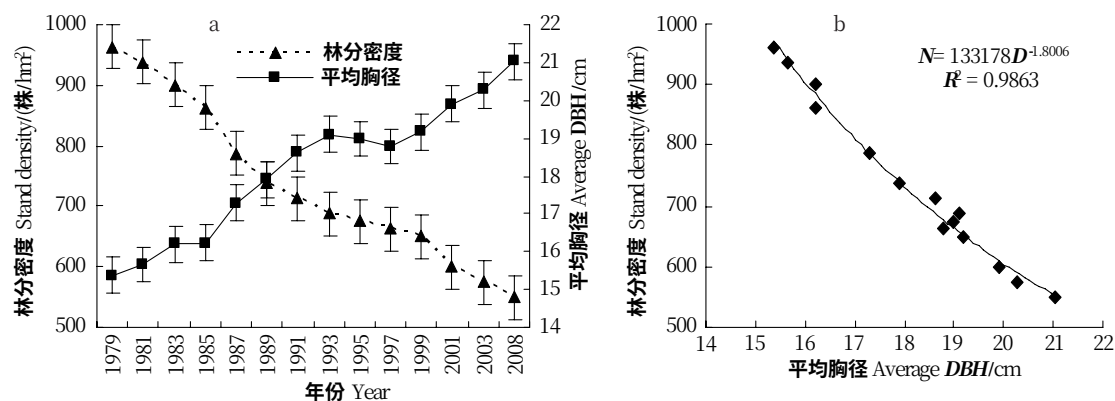


图 13 23 号标准地林分密度与平均胸径动态及相关关系

Fig. 13 Trend and correlativity of stand density and average DBH for No. 23 sample plot

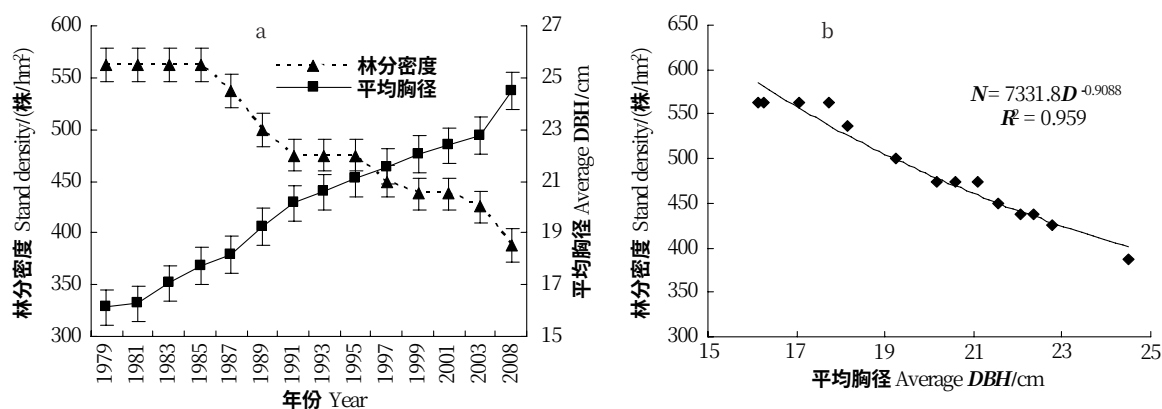


图 14 56 号标准地林分密度与平均胸径动态及相关关系

Fig. 14 Trend and correlativity of stand density and average DBH for No. 56 sample plot

进行模拟(图 16), 方程为 $N = 74699D^{-1.5938}$, R^2 为 0.9864, 相关性显著, β 值约为 1.5。

综合上述分析, 剔除存在人为干扰的 1、9、56 号林分; 对 22、23 号标准地的去除异常数据后进行模拟, 其结果也符合 $-3/2$ 幂自疏定律。由此可见: 白石砬子自然保护区天然林的自然稀疏规律明显, 符合 $-3/2$ 幂自疏定律; 并且 β 值是否恒定, 与立地、树种组成等因素无关, 与人为干扰有关。

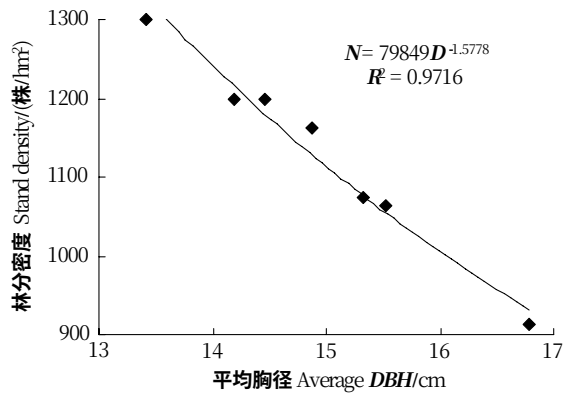


图 15 22 号标准地 1993—2008 年间林分密度与平均胸径相关关系

Fig. 15 Correlativity between stand density and average DBH of No. 22 sample plot from 1993 to 2008

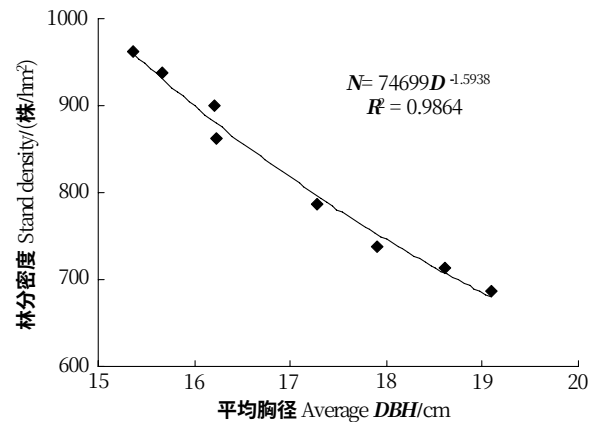


图 16 23 号标准地 1979—1993 年间林分密度与平均胸径相关关系

Fig. 16 Correlativity between stand density and average DBH of No. 23 sample plot from 1979 to 1993

2.5 天然林自然稀疏发生机制

由图 17 可见,各间隔期单位面积的枯损株数按直径分布均为左偏的单峰曲线,中小径阶枯损株数较多,大径阶木枯损株数较少。这种上层树木的优势不断的积累和放大,处于劣势的下层林木不断被淘汰现象,说明负反馈机制是直接导致自然那稀疏发生的根本原因,也说明光是影响森林群落自然稀疏主要因子。

3 讨论

3.1 $-3/2$ 自疏定律对天然林的适用性

植物种群的自然稀疏现象,在动力学机理上非常复杂,它反映了种群内个体之间存在着的种内与种间的相互作用。这种相互作用是非线性的,对于这类非线性的作用机制,人们经常采用幂律方程来描述。Reineke 与 Yoda 的表达式均为幂函数方程,且在研究林分自然稀疏规律时效果等同^[7]。两者主要差别是指标的选择,针对林业的特点,Zeide 认为利用林分密度与胸径这两个指标更准确,且胸径在林业调查中广泛使用,易于测量,准确性高^[41]。本文的研究结果表明,天然林自然稀疏过程符合 $-3/2$ 自疏法则, β 值恒定,而 β 值是否恒定,与立地、树种无关,与人为干扰有关。与 Ogawa 的研究结果一致,他们对栽植 20 a 的日本柳杉种群按时间序列进行自然稀疏规律研究,用 $\ln w = \ln K - \alpha \ln \rho$ 的表达式,其中 w 为平均树干体积, ρ 为密度,结果表明,随着林龄的增加,时间序列的斜率接近 $-3/2$,支持 $-3/2$ 自疏法则^[42]。Ogawa 用异速生长模型与时间序列相结合的方法,对日本扁柏根的平均生物量和密度的时间序列模型进行验证,支持 $-3/2$ 自疏法则,并认为:以前估计的最大密度线斜率的变化很大是因为用于估计最大密度线的时间不是自疏的时间,而只有找对时间才能有效估计出参数值^[43]。

3.2 $-3/2$ 自疏定律适用于天然林的合理性

$-3/2$ 自疏定律成立的基本条件是:群落由同龄、同种植物组成,且为单层结构;种群内生境条件均一;种群密度较大且随着生长过程的进行,自然稀疏发生而导致密度减少。天然林群落为异龄、复层结构,林冠重叠、被淘汰的是主林层下面的被压木,从理论上不符合 $-3/2$ 自疏法则的基本要求,但是从 $-3/2$ 自疏法则成立的生态学机理上,天然林自然稀疏过程具有符合规律 $-3/2$ 自疏法则的可能。

第一,负反馈机制是实现密度调控的动力学机制。负反馈机制在以往的林分稀疏模型研究中有所体现:

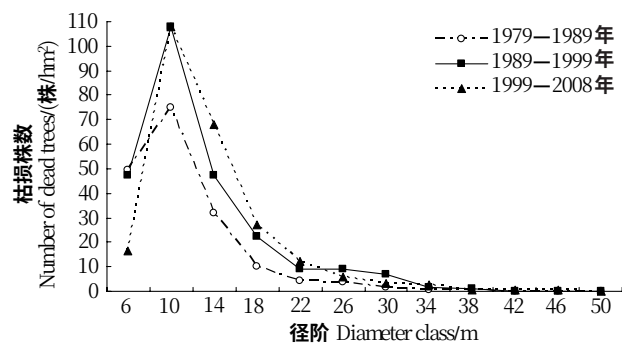


图 17 自然稀疏过程中枯损林木的直径结构

Fig. 17 Diameter structure of dead trees during self-thinning

逻辑斯蒂方程和 Gompertz 方程是典型的描述在有限资源条件下种群增长负反馈机制的数学方程;伊藤嘉昭提出了“植物种群重量增加的逻辑斯蒂性”的特点^[44];张大勇、江希钊以 $-3/2$ 自疏法则为依据,融合逻辑斯蒂方程和 Gompertz 方程,建立了林分自疏模型;唐首正在 Reineke 的密度指数概念基础上,提出了同龄纯林自然稀疏理论方程,可描述不同立木度林分自然稀疏规律,其中在完满立木度条件下,可推导出张大勇模型^[8-10]。本研究中,树木之间的负反馈作用表现为上层木优势的扩大和下层木的不断死亡。

第二,在 $-3/2$ 自然稀疏定律成立的基本假设条件中,强调的是由于空间资源的有限性所引起的物理或几何上的拥挤效应,对光照、水分等仅作为影响因子来考虑。对于天然林群落而言,光做为主要因素直接影响林冠下被压木的自然稀疏过程^[28,45]。植物之间存在非对称竞争^[1,30,42-43,45-46] 导致植物相邻个体间的相互影响不成比例。当它们共同对光竞争时,高的个体压迫小的个体,对小的个体植物单方面遮光,最后导致小个体低于光补偿点而死亡^[1-2,46]。本研究中,天然林内死亡林木的株数分布为左偏山状曲线,即随着时间变化生长小的个体植物将逐渐死亡,这种趋势支持非平衡竞争假说,并且与自疏是对光的竞争的结论相一致。

因此,本研究的结果为: $-3/2$ 自疏法则适用于自然演替的天然林。

3.3 天然林自然稀疏规律在森林生态系统管理中的应用

在气候变化的大背景下,典型自然保护区森林生态系统在排除了人为干扰因素后,其结构与功能的协调发展是受制于外界的气候等物理因素,还是决定于生命系统的自我调控?对该问题的回答是目前生态学研究及整个社会关注的热点。E. P. 奥德姆认为,如果种群或群落密度呈一定规律的变化,则被认为是生物系统的内因所控制的波动,如果密度的变化是不规律的,或明显地与某个重要的物理的限制因子相关,则是受外因控制,变化的结果是偏离稳定状态^[47]。

白石砬子自然保护区天然林林分具有连续的自然稀疏过程,被压木的小径阶林木逐渐被淘汰,且林分密度与平均胸径之间相关性明显,符合 $-3/2$ 自疏法则,表明自然保护区森林生态系统的自我调控能力较强,具有一定的稳定性。因此,在自然保护区森林生态系统管理过程中,应加强管理,尽可能的避免人为干扰,维持和保障森林生态系统的稳定性与可持续性。

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ACTA ECOLOGICA SINICA Vol. 31, No. 21 November, 2011 (Semimonthly)

CONTENTS

Landscape spatial analysis of a traditional tibetan settlement based on landscape pattern theory and feng-shui theory; the case of Zhagana, Diebu, Gansu Province	SHI Lisha, YAN Lijiao, HUANG Lu, et al (6305)
Temporal-spatial differentiation and its change in the landscape ecological security of Wuyishan Scenery District	YOU Weibin, HE Dongjin, WU Liyun, et al (6317)
Evaluation of eco-sustainability of roads in a tourism area; a case study within Yulong County	JIANG Yiyi (6328)
Study on the compactness assessment model of urban spatial form	ZHAO Jingzhu, SONG Yu, SHI Longyu, et al (6338)
A multi-scale analysis of red-crowned crane's habitat selection at the Yellow River Delta Nature Reserve, Shandong, China	CAO Mingchang, LIU Gaohuan, XU Haigen (6344)
Assessment and spatial distribution of water and soil loss in karst regions, southwest China	FAN Feide, WANG Kelin, XIONG Ying, et al (6353)
Construction of an eco-environmental database for watershed-scale data; an example from the Tarim River Basin	GAO Fan, YAN Zhenglong, HUANG Qiang (6363)
Reproductive allocation in dioecious shrub, <i>Rhamnus davurica</i>	WANG Juan, ZHANG Chunyu, ZHAO Xiuhai, et al (6371)
Age-dependent growth responses of <i>Pinus koraiensis</i> to climate in the north slope of Changbai Mountain, North-Eastern China	WANG Xiaoming, ZHAO Xiuhai, GAO Lushuang, et al (6378)
Fine-scale spatial point patterns of <i>Stipa krylovii</i> population in different alpine degraded grasslands	ZHAO Chengzhang, REN Heng, SHENG Yaping, et al (6388)
Community structure and population regeneration in remnant <i>Ginkgo biloba</i> stands	YANG Yongchuan, MU Jianping, TANG Cindy Q., et al (6396)
Reproductive characteristics and adaptive evolution of pin and thrum flowers in endangered species, <i>Primula merrilliana</i>	SHAO Jianwen, ZHANG Wenjuan, ZHANG Xiaoping (6410)
Leaf functional traits of four typical forests along the altitudinal gradients in Mt. Shennongjia	LUO Lu, SHEN Guozhen, XIE Zongqiang, et al (6420)
Reclaimed soil properties and weathered gangue change characteristics under various vegetation types on gangue pile	WANG Liyan, HAN Youzhi, ZHANG Chengliang, et al (6429)
Influence of fire on stands of <i>Pinus massoniana</i> in a karst mountain area of central Guizhou province	ZHANG Xi, CHUI Yingchun, ZHU Jun, et al (6442)
Morphological and physiological adaptation of <i>Caragana</i> species in the Inner Mongolia Plateau	MA Chengcang, GAO Yubao, LI Qingfang, et al (6451)
A comparative study on reasons of degenerated of <i>Haloxylon ammodendron</i> population in the western part of Gurbantunggut desert	SI Langming, LIU Tong, LIU Bin, et al (6460)
Self-thinning of natural broadleaved forests in Baishilazi Nature Reserve ...	ZHOU Yongbin, YIN You, YIN Mingfang, et al (6469)
Population status and dynamic trends of Amur tiger's prey in Eastern Wandashan Mountain, Heilongjiang Province	ZHANG Changzhi, ZHANG Minghai (6481)
The relationship between the occurrence of Colorado Potato Beetle, <i>Leptinotarsa decemlineata</i> , and rivers based on GIS: a case study of Shawan Country	LI Chao, ZHANG Zhi, GUO Wenchao, et al (6488)
Occurrence dynamics and trajectory analysis of <i>Cnaphalocrocis medinalis</i> Guenée in Xing'an Guangxi Municipality in 2010	JIANG Chunxian, QI Huihui, SUN Mingyang, et al (6495)
Adaptability of B-biotype <i>Bemisia tabaci</i> (Gennadius) to Host Shift	ZHOU Fucui, LI Chuanming, GU Aixiang, et al (6505)
Structural change analysis of cecal bacterial flora in different poultry breeds using PCR-DGGE ...	LI Yongzhu, Yongquan Cui (6513)
Effect of chicken manure-amended copper mine tailings on growth of three leguminous species, soil microbial biomass and enzyme activities	ZHANG Hong, SHEN Zhangjun, YANG Guide, et al (6522)
Physiological response of <i>Microcystis</i> to solar UV radiation	WANG Yan, LI Shanshan, LI Jianhong, et al (6532)
Relationship between cell volume and cell carbon and cell nitrogen for ten common dinoflagellates	WANG Yan, LI Ruixiang, DONG Shuanglin, et al (6540)
The community structure and abundance of microcystin-producing cyanobacteria in surface sediment of Lake Taihu in winter	LI Daming, KONG Fanxiang, YU Yang, et al (6551)
Influence of green belt structure on the dispersion of particle pollutants in street canyons	LIN Yinding, WU Xiaogang, HAO Xingyu, et al (6561)
Spatio-temporal variation analysis of urbanization and land use benefit of oasis urban areas in Xinjiang	YANG Yu, LIU Yi, DONG Wen, et al (6568)
Nitrate contamination and source tracing from NO_3^- - $\delta^{15}\text{N}$ in groundwater in Weifang, Shandong Province	XU Chunying, LI Yuzhong, LI Qiaozhen, et al (6579)
The impact of rising temperature on spring wheat production in the Yellow River irrigation region of Ningxia	XIAO Guoju, ZHANG Qiang, ZHANG Fengju, et al (6588)
A new hyperspectral index for the estimation of nitrogen contents of wheat canopy	LIANG Liang, YANG Minhua, DENG Kaidong, et al (6594)
The feature of N_2O emission from a paddy field in irrigation area of the Yellow River	ZHANG Hui, YANG Zhengli, LUO Liangguo, et al (6606)
Review and Monograph	
Research perspective for the effects of nitrogen deposition on biogenic volatile organic compounds	HUANG Juan, MO Jiangming, KONG Guohui, et al (6616)
Recruitment limitation of plant population: from seed production to sapling establishment	LI Ning, BAI Bing, LU Changhu (6624)
Scientific Note	
Response of anatomical structure and photosynthetic characteristics to low light stress in leaves of different maize genotypes	DU Chengfeng, LI Chaohai, LIU Tianxue, et al (6633)

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