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目 次

海洋生态资本理论框架下海洋生物资源的存量评估·····	任大川,陈 尚,夏 涛,等 (4805)
内生真菌对羽茅生长及光合特性的影响·····	贾 彤,任安芝,王 帅,等 (4811)
基于遥感图像处理技术胡杨叶气孔密度的估算及其生态意义·····	蒋圣淇,赵传燕,赵 阳,等 (4818)
水文变异下的黄河流域生态流量·····	张 强,李剑锋,陈晓宏,等 (4826)
黄河三角洲重度退化滨海湿地盐地碱蓬的生态修复效果·····	管 博,于君宝,陆兆华,等 (4835)
浙江省某 PCBs 废物储存点对其邻近滩涂生态系统的毒性风险·····	何闪英,陈昆柏 (4841)
鄱阳湖苔草湿地甲烷释放特征·····	胡启武,朱丽丽,幸瑞新,等 (4851)
三峡库区银鱼生长特点及资源分析·····	邵晓阳,黎道峰,谭 路,等 (4858)
低温应激对吉富罗非鱼血清生化指标及肝脏 HSP70 基因表达的影响 ···	刘 波,王美姝,谢 骏,等 (4866)
Cd ²⁺ 对角突臂尾轮虫和曲腿龟甲轮虫的急性毒性和生命表统计学参数的影响 ·····	许丹丹,席貽龙,马 杰,等 (4874)
圈养梅花鹿 BDNF 基因多态性与日常行为性状的关联分析 ·····	吕慎金,杨 燕,魏万红 (4881)
华北平原玉米田生态系统光合作用特征及影响因素 ·····	同小娟,李 俊,刘 渡 (4889)
长期施肥对麦田大型土壤动物群落结构的影响 ·····	谷艳芳,张 莉,丁圣彦,等 (4900)
蚯蚓对湿地植物光合特性及净化污水能力的影响·····	徐德福,李映雪,王让会,等 (4907)
三种农药对红裸须摇蚊毒力和羧酸酯酶活性的影响 ·····	方国飞 (4914)
六星黑点豹蠹蛾成虫生殖行为特征与性趋向·····	刘金龙,宗世祥,张金桐,等 (4919)
除草剂胁迫对空心莲子草叶甲种群的影响及应对策略·····	刘雨芳,彭梅芳,王成超,等 (4928)
荒漠植物准噶尔无叶豆结实、结籽格局及其生态适应意义 ·····	施 翔,王建成,张道远,等 (4935)
限水灌溉冬小麦冠层氮分布与转运特征及其对供氮的响应·····	蒿宝珍,姜丽娜,方保停,等 (4941)
准噶尔盆地梭梭、白梭梭植物构型特征 ·····	王丽娟,孙栋元,赵成义,等 (4952)
基于地表温度-植被指数关系的地表温度降尺度方法研究 ·····	聂建亮,武建军,杨 曦,等 (4961)
岩溶区不同植被类型下的土壤氮同位素分异特征 ·····	汪智军,梁 轩,贺秋芳,等 (4970)
施氮量对麻疯树幼苗生长及叶片光合特性的影响 ·····	尹 丽,胡庭兴,刘永安,等 (4977)
黄土丘陵区羔沟流域典型植物叶片 C、N、P 化学计量特征季节变化 ·····	王凯博,上官周平 (4985)
克隆整合提高淹水胁迫下狗牙根根部的活性氧清除能力·····	李兆佳,喻 杰,樊大勇,等 (4992)
低覆盖度固沙林的乔木分布格局与防风效果·····	杨文斌,董慧龙,卢 琦,等 (5000)
东灵山林区不同森林植被水源涵养功能评价·····	莫 菲,李叙勇,贺淑霞,等 (5009)
11 种温带树种粗木质残体分解初期结构性成分和呼吸速率的变化 ·····	张利敏,王传宽,唐 艳 (5017)
连栽第 1 和第 2 代杉木人工林养分循环的比较·····	田大伦,沈 燕,康文星,等 (5025)
最优化设计连续的自然保护区·····	王宜成 (5033)
基于自然地理特征的长江口水域分区·····	刘录三,郑丙辉,孟 伟,等 (5042)
煤电一体化开发对锡林郭勒盟环境经济的影响·····	吴 迪,代方舟,严 岩,等 (5055)
专论与综述	
生态条件的多样性变化对蜜蜂生存的影响·····	侯春生,张学锋 (5061)
研究简报	
胶州湾潮间带大型底栖动物次级生产力的时空变化·····	张崇良,徐宾铎,任一平,等 (5071)
湿地公园研究体系构建·····	王立龙,陆 林 (5081)
基于生态足迹的半干旱草原区生态承载力与可持续发展研究——以内蒙古锡林郭勒盟为例·····	杨 艳,牛建明,张 庆,等 (5096)
学术信息与动态	
恢复与重建自然与文化的和谐——2011 生态恢复学会国际会议简介 ···	彭少麟,陈蕾伊,侯玉平,等 (5105)
期刊基本参数:CN 11-2031/Q * 1981 * m * 16 * 302 * zh * P * ¥ 70.00 * 1510 * 37 * 2011-09	



封面图说: 相当数量的降雪与低温严寒是冰川发育的主要因素,地球上的冰川除南北两极外,只有在高海拔的寒冷山地才能存在。喜马拉雅山造山运动使中国成为了世界上中低纬度冰川最为发育的国家,喜马拉雅山地区雪峰连绵、冰川四溢,共有现代冰川 17000 多条,是世界冰川发育的中心之一。

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

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荒漠植物准噶尔无叶豆结实、结籽格局 及其生态适应意义

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摘要: 连续 2a 采用野外记录的方式对荒漠植物准噶尔无叶豆的结实、结籽格局进行了比较研究。结果表明: 植株内花序生成格局表现为不同大小的花序在总花序中的比重与其结实率存在显著正相关, 其中含有中等花数目的花序所占的比重及其结实率均最高, 此种分布格局能够最大程度的保证繁殖成功; 果序内果实生成格局表现为单花着生位置 (从近柄端算起) 与其结实量占总结实量的比例成线性负相关, 花序基部的结实比例最高, 顶部结实比例近为 0; 荚果内种子生成格局表现为: 中间位置的胚珠败育率最低。另外, 年际间荚果内仅有 (1.08 ± 0.03) 粒和 (1.07 ± 0.03) 粒种子能够完全成熟, 此种结籽格局是准噶尔无叶豆保证后代质量的最佳策略。

关键词: 准噶尔无叶豆; 结实格局; 结籽格局; 繁殖成功

Patterns of fruit and seed production and ecological significance in desert species *Eremosparton songoricum* (FABACEAE)

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Abstract: Plant reproductive modules include flowers, inflorescences, fruits and seeds, and also the reproductive branches that bear these plant parts, which have certain distribution pattern and quantitative change dynamics. Selective abortion is one of the sources of seed plant fruiting and seeding patterns. In order to determine the patterns of fruit production among and within inflorescences, seed production within pods, and further examine the evolutionary, ecological significance of selective abortion in a desert species *Eremosparton songoricum* (Litv.) Vass., we did our research over two years in a wild population in the north edge of Gurbantunggut Desert, Xinjiang, China. To record the fruit production among inflorescences, 141 and 105 inflorescences from twenty individual plants were randomly chosen in 2007 and 2008, respectively. Fruit development and position within each inflorescence were monitored daily, and the number of completely mature fruits within each inflorescence was counted to get the frequency distribution and the fruit set of different inflorescence sizes. To determine percentage of fruit production from basal position to distal position within the inflorescences, 100 inflorescences with 16 and 13 flowers were chosen in 2007 and 2008, respectively. To determine the

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seed production within pods, 300 completely mature fruits were randomly chosen in 2007 and 2008 to monitor the seed production from basal position to distal position within each pod. Results showed that the frequency distribution and fruit set of different inflorescence sizes were positively correlated, with the middle inflorescence size being the most frequent and also having the highest fruit set, which appears to be the optimal reproductive strategy; The flowers from the basal position of an inflorescence were more likely to set fruit, which appears to maintain the reproductive success from the adaptive strategy angle, and the percentage of fruit production at the distal position of an inflorescence was approximately zero which may be make up to the loss of basal flowers of an inflorescence caused by desert weather condition or distal flower may play more important role in male function for attracting more insects rather than bearing fruit; Ovules from the middle position within an ovary were more likely to produce seed. There were an average of only 1.08 ± 0.03 and 1.07 ± 0.03 seeds matured per pod in 2007 and 2008, respectively. Producing one seed per pod may be the optimal strategy in this limited resource desert situation, with the single seed appearing to be of higher quality (16.23 ± 0.30) mg than those derived from multi-seed pods (18.44 ± 0.32) mg. Also, a single seeded pod, compared with two or three seeds within one pod, can lower the weight of the dispersal fruit unit, which will improve the dispersal distance and then play an important role in occupying new habitats for this rare species.

Key Words: *E. songoricum*; fruiting pattern; seeding pattern; reproductive success

高等植物的花、花序、果实和种子,甚至着生这些器官的生殖枝均可称为生殖构件^[1],这些生殖构件呈现一定的分布格局和数量动态变化^[2-6]。种子植物的结实、结籽格局中,果实和种子的败育可分为随机败育和选择性败育。国内外许多研究学者都曾针对选择性败育的现象,原因及其生态进化意义进行了深入的探讨^[7-9]。选择性败育包括果实和种子两种选择性败育现象。花序从基部向顶部顺次开放的植物中,果实败育格局有两种类型,多数表现为花序基部向顶部结实率逐渐下降^[10-13],少数表现为花序中部^[14]或顶部^[15]结实率最高。在果实内种子呈线性排列的植物中,种子的选择性败育包括有3种类型,第一类为选择果实花梗端或基部的种子败育^[16-17];第二类为选择性地败育果实柱头端和基部的种子而成熟果实中部的种子^[18];第三类为选择性地败育果实柱头端的种子^[19-20]。对于选择性败育的原因,被普遍接受的包括有资源限制、传粉限制、同胞竞争、虫食作用等^[21-22],但是每种原因造成果实或种子败育所占的比例很难进行量化分析。选择性败育的生态进化意义在于首先其可以提高母本及后代的适合度^[23-24],其次在于其对于果实的扩散具有重要意义,因此成熟含有少量种子的果实具有更高的适合度^[25]。

准噶尔无叶豆系豆科无叶豆属多年生小半灌木,稀有种^[26],在我国仅片断化分布于新疆古尔班通古特沙漠局部区域的流动—半流动沙丘上^[27]。2004—2006 年对自然种群的调查中发现该物种是兼性克隆植物,花序为向顶式开放,其单株开花数 200—3000 朵不等,结实率低于 16%^[28],远低于自交亲和两性花植物 72% 的结实率^[29];种子在果实内呈线性排列,结籽率低于 16%^[28],远低于大多数两性花植物 50%—85% 的结籽率,可见该种有性生殖环节存在障碍。本文重点从物种生殖分配的角度出发,通过对其植株内花序间、果序内和荚果内不同部位的结实、结籽数量进行观察统计,拟重点研究:(1)准噶尔无叶豆自然种群花序间结实格局;(2)准噶尔无叶豆自然种群果序内的结实格局;(3)准噶尔无叶豆自然种群荚果内结籽格局;并进一步分析探讨结实、结籽格局的生态进化意义,本研究有助于该物种保育工作的开展,同时还有助于深入理解其他荒漠植物的繁殖策略。

1 研究地区概况和研究方法

1.1 研究地区概况

研究地点位于古尔班通古特沙漠最北缘的阿勒泰地区富蕴县杜热乡境内的半流动沙丘($46^{\circ}31'05''$ N, $88^{\circ}33'04''$ E, 海拔 662m, 面积 $280\text{m} \times 30\text{m}$)。古尔班通古特沙漠干旱少雨,温差大,蒸发强烈,因此该地区属于典型的温带内陆荒漠性质^[30]。准噶尔无叶豆种群 6 月初开花,6 月底花期结束;叶为退化状,长总状花序多互

生于叶腋;果实 7 月间开始成熟,8 月底果期结束。准噶尔无叶豆果实发育初期,荚果内多具有 2—3 枚受精的胚珠,荚果发育成熟后多数仅其中一枚能够发育成熟。野外调查及试验在 2007—2008 年的 6 月至 8 月间进行。

1.2 花序间结实格局

2007 年和 2008 年分别随机标记 20 株植株,并从中随机选择 141 和 101 个花序(原始分别标记了 200 个花序,部分花序在发育过程中遭到自然或人为因素的破坏),果实开始发育时每日观察果实形态以及在花序中着生的位置,统计每个花序中完全成熟的果实的数目(脱落的幼嫩的果荚不能正常发育),并且根据花序上的花痕数目统计每个花序的花数目,并计算不同大小的花序(Different inflorescence sizes)的比重和结实率,比重=不同大小的花序的数量/总花序数 $\times 100\%$;结实率=结实量/花数目 $\times 100\%$ 。

1.3 果序内结实格局

2007 年和 2008 年分别标记 100 个均含有 16 朵花和 13 朵花的花序进行标记(2007 年生成的花序大小普遍大于 2008 年的花序)。参照果序间成熟果实的统计方法,计算不同年际间果序内部从近柄端(1)至远端各位置的结实比例,结实比例=各位置的总结实量/所有位置的总结实量 $\times 100\%$ 。

1.4 荚果内结籽格局

2007 年和 2008 年分别随机选择 300 个成熟的果实,在体式显微镜下用解剖刀将果皮小心打开,将近果柄端的位置记为“1”,对每粒果荚内的种子成熟的位置以及胚珠数目进行记录统计。

1.5 数据分析

所有数据用 SPSS17.0 进行分析,用 Origin 7.5 作图。用 Bivariate Correlations 来进行不同大小花序的比重与结实率的相关性分析;用 Linear Regression 来建立果序内部从近柄端至远端各位置的结实量占总结实量的比例的线性回归方程;胚珠位置与结籽数目的二次回归方程用 Curve Estimation 来建立。数据的正态性根据 Kolmogorov-Smirnov 指数和 Shapiro-Wilk 指数综合考虑,方差齐性检验用 Levene 检验法。

2 结果与分析

2.1 花序间结实格局

准噶尔无叶豆花序大小分布在 2—19 朵花之间,2007 年和 2008 年(图 1)均倾向于生成含有中等花数量(7—14)的花序,含有少量花(<5)和含有大量花(>14)的花序所占的比重较低;含有中等花数量的花序的结实率也普遍较高。并且经过 Bivariate Correlations 分析后发现,植株内不同大小的花序在总花序中的比重与其结实率在年际间均成显著正相关($P=0.026$; 0.012)。

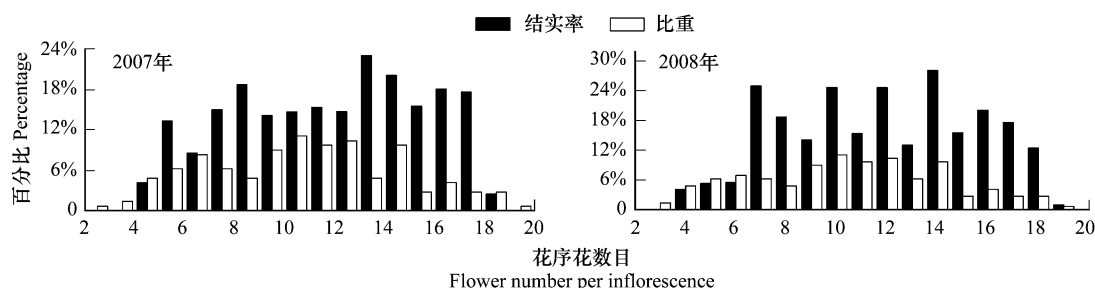


图 1 准噶尔无叶豆 2007 年和 2008 年不同大小的花序的比重与结实率的相关性

Fig. 1 The correlation between frequency distribution of inflorescence size and the fruit set in *E. songoricum* from 2007 to 2008

2.2 果序内结实格局

2007 年和 2008 年(图 2)单花着生位置(从近柄端算起)与其结实量占总结实量的比例成线性负相关,花序基部的结实比例最高,顶部结实比例近为 0。

2.3 荚果内结籽格局

2007 年和 2008 年(图 3)单粒荚果分别生成(8.31 ± 0.12)和(8.38 ± 0.11)枚胚珠,仅有(1.08 ± 0.03)和

(1.07 ± 0.03) 粒种子能够完全成熟。荚果内结籽格局均表现为荚果内部中间位置的胚珠败育率最低, 经过 Curve Estimation 分析后发现, 胚珠位置与结籽数目均与二次回归方程拟合较好 ($R^2 = 0.774$; 0.737)。

3 讨论

准噶尔无叶豆植株内含有中等花数目的花序所占比重最高, 而此种花序类型的结实率也是最高的, 此种分布格局最大程度地保证了繁殖成功, 这与 Lack^[31] 的研究结果一致。

Ohara 和 Higashi^[32] 对罂粟科植物 *Corydalis ambigua* 的研究结果相反: 具有较大花展示的花序的结实率最高, 但是植株更加倾向于产生具有较小花展示的花序, 有限的资源可能是 *C. ambigua* 此种花序生成格局重要的选择力量。对于准噶尔无叶豆来说, 较大的花展示有利于吸引传粉者, 昆虫访花频率更高^[33], 植株似乎应该倾向于生成大的花展示来增加花粉转移的机会, 但是植株花序的大小必须建立在用于产生吸引结构的有效资

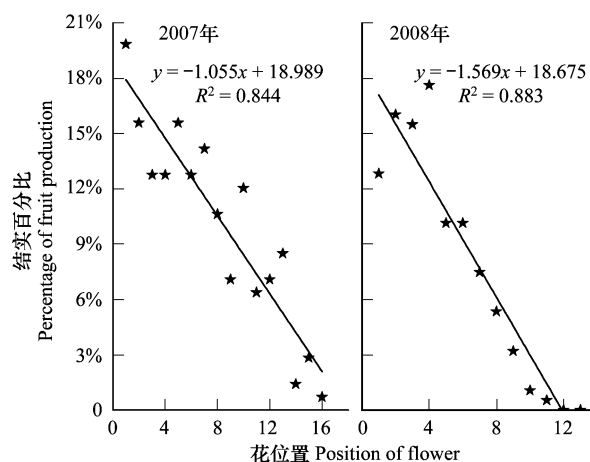


图2 自然状态下准噶尔无叶豆 2007 年和 2008 年果序内部从近柄端至远端各位置的结实量占总结实量的比例

Fig. 2 The percentage of fruit production from basal position to distal position within the inflorescence in *E. songoricum* from 2007 to 2008 under natural condition

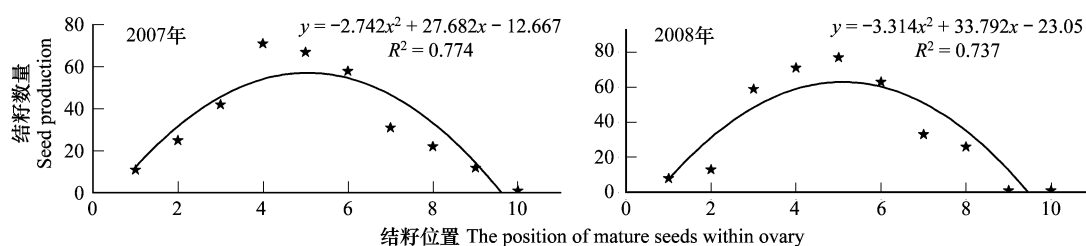


图3 自然状态下准噶尔无叶豆 2007 年和 2008 年荚果内部从近柄端至远端各位置的结籽量变化

Fig. 3 The variation of seed production from basal position to distal position within the pod in *E. songoricum* in 2007 and 2008 under natural condition

源和用于成熟果实的有效资源两方面的权衡基础之上^[34-36]。资源有限是准噶尔无叶豆结实的主要影响因素之一^[37], 大的花展示无疑会增加投资, 准噶尔无叶豆在资源有限的选择压力下, 选择更多得生成含有中等花数目的花序是保障对传粉者的吸引力的基础上提高结实率的最佳策略。

关于果序内败育格局的研究, 准噶尔无叶豆花序基部至顶部结实率呈递减趋势。关于此种结实格局存在两种最普遍的假说: 资源竞争^[21,38] 和构造效应^[39-41]。资源竞争假说即花序内的子房竞争有限的资源, 发育早和(或)空间位置接近资源的果实比后发育和位于资源远端的果实获得更多的资源^[25]。构造效应假说即花序内部存在对于不同位置的繁殖成功率的构造限制, 其花序末端的结实率不会因为剔除基部花而发生改变^[14]。另外不同部位接收到的花粉质量和(或)数量的差异也可能是造成此种结实格局的原因之一^[42]。对于准噶尔无叶豆来说, 养分贫瘠的沙质土壤不能为其提供足够的资源^[28], 补充养分和剔除部分花芽和果荚均能显著提高结实率^[37], 因此认为资源限制是造成果实败育的合理解释。但是基部至顶部结实比例呈现下降趋势, 可能是因为准噶尔无叶豆生成一个果实比生成一朵花消耗更多的资源^[37], 果序基部的果实先发育, 其主要与花形成竞争, 能获取更多的母本资源, 这些果实因而更容易成熟^[43-44]; 顶部的果实后发育, 主要与果实进行竞争, 竞争所得资源有限, 不能满足果实成熟的条件, 这是基部果实存在的时间优势。另一方面, 当供给繁殖的资源有限时, 植株上距光合产物源和营养源最近的果实存在对资源竞争的空间优势。时间与空间优势的综合作用, 使得准噶尔无叶豆形成花序基部的结实比例最高, 顶部结实比例近为 0 的结实格局。这与

Guitián^[45]在 *Prunus mahaleb* 和 Medrano 等^[21]在 *Pancratium maritimum* 中发现的结果相一致。从适应策略来理解,准噶尔无叶豆花序基部的花是保证繁殖成功的必要,一方面,顶部的花是为了补偿基部花的损失,此种空间效应可能是为了抵御沙漠大风和高温天气给先期发育果实造成干扰的一种补偿效应;另一方面,顶部的花可能对发挥雄性功能作用更大,因为其可能更多的用于昆虫向其他植株转运花粉^[29]。

关于荚果内种子败育格局的研究,在豆科植物中较多的文献对种子形成与所处的胚珠位置进行了研究,但研究结果不尽相同。准噶尔无叶豆的结籽格局表现为果荚内中间位置的胚珠更容易形成种子,这与 Link^[46]对豆科植物 *Pisum sativum* 的研究结果一致。选择性败育荚果内的种子可以有效提高后代的适合度,其可能是某些生活在资源贫乏、干旱少雨条件下的植物在长期进化过程中形成的一种生殖保障^[47]。准噶尔无叶豆荚果内形成多粒种子的平均单粒种子重量 (16.23 ± 0.30) mg 远低于荚果内仅形成一粒种子的重量 (18.44 ± 0.32) mg,因此认为荚果内仅形成 1 粒种子是为了达到最佳种子质量所形成的适应策略^[37]。另外,荚果内仅形成一粒种子相对于生成 2—3 粒种子,明显降低了以果实作为扩散单位的重量,这样将有利于传播距离的扩大,对种群占领新生境具有一定的意义。

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CONTENTS

Marine ecological capital: valuation of standing stock of marine living resources	REN Dachuan, CHEN Shang, XIA Tao, et al (4805)
Effect of Endophytic fungi on growth and photosynthetic characteristics of <i>Achnatherum sibiricum</i>	JIA Tong, REN Anzhi, WANG Shuai, et al (4811)
Based on image processing technology estimating leaves stomatal density of <i>Populus euphratica</i> and analysis of its ecological significance	JIAN Shengqi, ZHAO Chuanyan, ZHAO Yang, et al (4818)
Evaluation of the ecological instream flow in the Yellow River basin with hydrological alterations	ZHANG Qiang, LI Jianfeng, CHEN Xiaohong, et al (4826)
The ecological effects of <i>Suaeda salsa</i> on repairing heavily degraded coastal saline-alkaline wetlands in the Yellow River Delta	GUAN Bo, YU Junbao, LU Zhaohua, et al (4835)
Toxicity risks to the closed tidal flat ecosystem of a PCBs waste savepoint at the coast of Zhejiang	HE Shanying, CHEN Kunbai (4841)
Methane emission from a <i>Carex</i> -dominated wetland in Poyang Lake	HU Qiwu, ZHU Lili, XING Ruixin, et al (4851)
The study on Ice-fish Resources in the Three Gorges Reservoir	SHAO Xiaoyang, LI Daofeng, TAN Lu, et al (4858)
Effects of acute cold stress on serum biochemical and immune parameters and liver HSP70 gene expression in GIFT strain of Nile tilapia (<i>Oreochromis niloticus</i>)	LIU Bo, WANG Meiyao, XIE Jun, et al (4866)
Acute toxicity and effect of Cd ²⁺ on life table demography of <i>Brachionus angularis</i> and <i>Keratella valga</i>	XU Dandan, XI Yilong, MA Jie, et al (4874)
The association of BDNF gene polymorphisms with normal behavior traits in house-hold sika deer (<i>Cervus nippon</i>)	LÜ Shenjin, YANG Yan, WEI Wanhong (4881)
Characteristics and controlling factors of photosynthesis in a maize ecosystem on the North China Plain	TONG Xiaojuan, LI Jun, LIU Du (4889)
The soil macrofaunal community structure under a long-term fertilization in wheat field	GU Yanfang, ZHANG Li, DING Shengyan, et al (4900)
Effect of earthworms on the photosynthetic characteristics of wetland plants and their capacity to purify wastewater	XU Defu, LI Yingxue, WANG Ranghui, et al (4907)
Toxicity of three pesticides and their effects on carboxylesterase activity of <i>Propiloscerus akamusi</i>	FANG Guofei (4914)
Reproductive behavior character and sexual tendency of the adult <i>Zeuzera leuconotum</i> Butler (Lepidoptera: Cossidae)	LIU Jinlong, ZONG Shixiang, ZHANG Jintong, et al (4919)
Effects of herbicides stress on the population of alligator weed flea beetles, <i>Agasicles hygrophila</i> (Col.: Chrysomelidae) and corresponding strategies	LIU Yufang, PENG Meifang, WANG Chengchao, et al (4928)
Patterns of fruit and seed production and ecological significance in desert species <i>Eremosparton songoricum</i> (FABACEAE)	SHI Xiang, WANG Jiancheng, ZHANG Daoyuan, et al (4935)
Effect of different nitrogen supply on the temporal and spatial distribution and remobilization of canopy nitrogen in winter wheat under limited irrigation condition	HAO Baozhen, JIANG Lina, FANG Baoting, et al (4941)
Plant architecture characteristics of <i>Haloxylon ammodendron</i> and <i>Haloxylon persicum</i> in Zhungar Basin	WANG Lijuan, SUN Dongyuan, ZHAO Chengyi, et al (4952)
Downscaling land surface temperature based on relationship between surface temperature and vegetation index	NIE Jianliang, WU Jianjun, YANG Xi, et al (4961)
Differential characteristics of soil δ ¹⁵ N under varying vegetation in karst areas	WANG Zhijun, LIANG Xuan, HE Qiufang, et al (4970)
Effect of nitrogen application rate on growth and leaf photosynthetic characteristics of <i>Jatropha curcas</i> L. seedlings	YIN Li, HU Tingxing, LIU Yongan, et al (4977)
Seasonal variations in leaf C, N, and P stoichiometry of typical plants in the Yangou watershed in the loess hilly gully region	WANG Kaibo, SHANGGUAN Zhouping (4985)
Clonal integration enhances the ability to scavenge reactive oxygen species in root of <i>Cynodon dactylon</i> subjected to submergence	LI Zhaojia, YU Jie, FAN Dayong, et al (4992)
Pattern of flow-covered sand-fixing woodland and its windbreak effect	YANG Wenbin, DONG Huilong, LU Qi, et al (5000)
Evaluation of soil and water conservation capacity of different forest types in Dongling Mountain	MO Fei, LI Xuyong, HE Shuxia, et al (5009)
Changes in structural components and respiration rates of coarse woody debris at the initial decomposition stage for 11 temperate tree species	ZHANG Limin, WANG Chuankuan, TANG Yan (5009)
Characteristics of nutrient cycling in first and second rotations of Chinese fir plantations	TIAN Dalun, SHEN Yan, KANG Wenxing, et al (5025)
The optimal design of a connected nature reserve network	WANG Yicheng (5033)
Sub-areas compartmentalization of Changjiang Estuary based on the natural geographical characteristics	LIU Lusan, ZHENG Binghui, MENG Wei, et al (5042)
The environmental and economic influence of coal-electricity integration exploitation in the Xilingol League	WU Di, DAI Fangzhou, YAN Yan, et al (5055)
Review and Monograph	
The influence of diversity changes of ecological conditions on the survival of honey bees	HOU Chunsheng, ZHANG Xuefeng (5061)
Scientific Note	
The spatio-temporal change in the secondary production of macrozoobenthos in the intertidal zone of Jiaozhou Bay	ZHANG Chongliang, XU Binduo, REN Yiping, et al (5071)
The studying system construction of wetland parks	WANG Lilong, LU Lin (5081)
Ecological footprint analysis of a semi-arid grassland region facilitates assessment of its ecological carrying capacity: a case study of Xilinguole League	YANG Yan, NIU Jianming, ZHANG Qing, et al (5096)

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