ABSENCE OF TREE SEEDS IMPEDES SHRUBLAND SUCCESSION IN SOUTHERN CHINA

J Wang^{1, 2}, C Zou³, H Ren^{1,*}, WJ Duan¹

¹Heshan National Field Research Station of Forest Ecosystem, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China ²Graduate University of the Chinese Academy of Sciences, Beijing, China

³Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA

Received May 2008

WANG J, ZOU C, REN H & DUAN WJ. 2009. Absence of tree seeds impedes shrubland succession in southern China. Change in landuse in southern China has resulted in the abandonment of over 40 million ha of degraded grazing pasture and cultivated farmland, which have consequently converted to shrubland. Shrubland has low economic value and provides limited ecosystem services but is now the dominant vegetation in three provinces of southern China. Effective management of such shrubland ecosystem requires improved understanding of many ecological factors, including sources of viable seeds in the soil seed bank and the interaction between the seed bank and the current vegetation. We investigated the soil seed bank in a shrubland using a seedling germination assay, and compared the species composition in the shrubland was high, the Sorensen's coefficient and species richness in the soil seed bank were low. The soil seed bank was mainly dominated by grass and shrub species; no pine or other indigenous tree seeds were detected. Our findings suggest that the limited seed source of tree species is one of the primary factors slowing or stopping secondary succession in southern China. Direct planting of tree seedlings may facilitate secondary succession in the severely degraded shrublands.

Keywords: Degraded grassland, indigenous species, secondary regeneration, restoration

WANG J, ZOU C, REN H & DUAN WJ. 2009. Ketiadaan biji benih pokok menghalang sesaran di tanah semak di selatan negara China. Perubahan penggunaan tanah di selatan negara China mengakibatkan lebih 40 juta hektar padang rumput ternak dan tanah ladang usang terbiar dan akhirnya bertukar menjadi tanah semak. Tanah semak mempunyai nilai ekonomi yang rendah dan sumbangannya terhadap ekosistem terhad. Kini, belukar ialah vegetasi dominan di tiga buah wilayah di selatan negara China. Pengurusan ekosistem tanah semak yang berkesan memerlukan pemahaman yang lebih baik tentang faktor ekologi seperti sumber biji benih berdaya hidup dalam bank biji benih tanah dan interaksi antara bank biji benih dengan vegetasi semasa. Bank biji benih tanah di tanah semak dikaji menggunakan ujian percambahan biji benih. Komposisi spesies dalam bank biji benih dibandingkan dengan vegetasi komuniti menggunakan koefisien Sorensen. Kepadatan bank biji benih di tanah semak tinggi tetapi koefisien Sorensen dan kekayaan spesiesnya rendah. Bank biji benih tanah di dominasi oleh spesies-spesies rumput dan pokok renek. Biji benih pokok pain atau biji benih pokok asli tidak dicerap. Keputusan mencadangkan bahawa sumber biji benih spesies pokok yang terhad merupakan salah satu faktor utama yang melambat atau memberhentikan sesaran sekunder di selatan negara China. Penanaman terus anak benih pokok mungkin dapat mempercepat sesaran sekunder di tanah semak yang dinyahgred dengan teruk.

INTRODUCTION

The vegetation of south-eastern China has been under dramatic change. In the last half century, most forests in this region were converted into agricultural fields or pastures (Peng 2003), which have become severely degraded due to intensive cultivation and overgrazing. Such degraded agricultural fields and pastures cover about 47 million ha and occupy about 78% of the total land area of Guangdong, Fujian and Guangxi provinces (Yu & Peng 1996, Ren *et al.* 2007a). The vegetation climax community in this region, broadleaf evergreen forest, has been reduced to remnant fragments with a total area of only 1.07 million ha. Recently, most of these degraded agricultural fields and pastures were no longer of production or grazed or cultivated because of economic transformation and increasing environmental concerns. Once abandoned, these old fields were quickly invaded and taken over by shrub species (Li *et al.* 2003).

Previous studies of shrublands near original forests have indicated that Pinus massoniana (a native, wind-dispersed species of pine) usually establishes itself as a pioneer tree species in the shrubland, leading to the formation of a significant overstorey in which pine is the main or only tree species (Dong 1987, Latham 2003, Peng 2003). By providing perches for birds that disperse seeds of native broadleaf species (Ashton et al. 1997, Toh et al. 1999) and by modifying the below-canopy environment (Zou et al. 2007), an extensive pine overstorey should facilitate the establishment of shadetolerant indigenous broadleaf evergreen tree species that will eventually overgrow the pine and form a broadleaf evergreen forest. However, field observations on shrubland not adjacent to indigenous forest showed that this succession seems to stop at the shrubland stage and that trees do not establish even after two decades (Ren & Peng 2001). Shrubland in southern China provides almost no economic value and limited ecosystem service (Cai et al. 1996, Li et al. 2003, Ren et al. 2007b), and the pressure to restore these degraded lands is high. So, facilitating and accelerating this secondary regeneration process (the conversion of shrubland into forest) is now a priority in this region.

The soil seed bank is an important component of a plant community, reflecting both the existing vegetation structure currently associated with the site (Pugnaire & Lazaro 2000) and also the potential for new species to establish and grow into the canopy (Kalamees & Zobel 2002). In many ecosystems, arrested succession may result from either lack of viable seeds in the soil seed bank or unfavourable germination conditions (Zhang et al. 2001, Cohen et al. 2004). Since management approaches to correct these two causes are completely different, it is critical to understand the composition of the soil seed bank and its relationship with the aboveground vegetation community at the shrubland stage. In the soil seed bank, the persistent components are commonly assumed to serve as buffers against environmental variability (Hyatt & Casper 2000, Satterthwaite *et al.* 2007), and therefore the abundance of persistent seeds will greatly influence the success of management and restoration (Davies & Waite 1998, Luzuriaga *et al.* 2005). As noted earlier, lack of seeds of desirable species in the persistent seed banks (Zimmerman *et al.* 2000) or environmental limitation during seedling establishment (Hau & Corlett 2003) may prevent successful colonization by indigenous tree species in many ecosystems. We hypothesized that similar causes might explain the failure of indigenous tree species in colonizing shrubland in southern China.

As part of a larger project to restore severely degraded shrubland ecosystem, this study focused on the species composition and richness of the soil seed bank. Specifically, this study attempted to answer the following questions: (1) How large is the soil seed bank and which species does it contain? (2) How significant is the seed bank in maintaining the species diversity of the shrubland community? (3) Is absence of seeds of tree species in the soil seed bank the likely reason for the absence of both pine and indigenous broadleaf tree species? Answers to these questions should provide insights into the vegetation dynamics in shrublands and should help forest managers restore the ecosystem.

MATERIALS AND METHODS

Study site

The study site was located at the Heshan Hilly Land Interdisciplinary Experimental Station, Chinese Academy of Sciences (112° 54' E, 22° 41' N). This site is characterized by a typical southern subtropical monsoon climate with a mean annual temperature of 21.7 °C. The mean annual rainfall is 1700 mm and concentrated between May and September. The soil is laterite. The experimental plot was a 3.5 ha shrubland dominated by Ilex asprella, Evodia lepta and Trema tomentosa, with a total of 15 Masson pines (Pinus massoniana) and no broadleaf tree species. This site was dominated by two grass species (Ischaemum indicum and Eriachne pallescens) before it was abandoned 22 years ago. The closest, wellprotected natural vegetation is at Dinghushan Mountain, about 70 km to the north. The location and the current vegetation of the study site are shown in Figure 1.

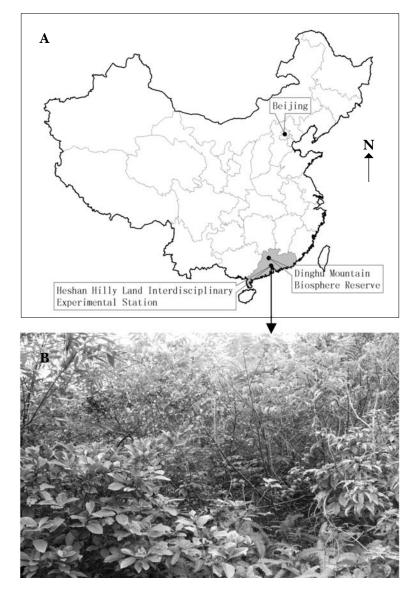


Figure 1 Locations of the (A) study site and the Dinghu Mountain Biosphere Reserve (about 70 km away from the studied shrubland) and (B) dense shrubland at Heshan Hilly Land Interdisciplinary Experimental Station, Guangdong Province, China

Soil sampling, germination assay and field survey

Three quadrats (5 × 30 m each) were set up to represent the upper, middle and base locations along a shrubland slope. Each quadrat was subdivided into six 5 × 5 m grids with one subplot (1 × 1 m) located at the centre of each grid. Six soil samples of $10 \times 10 \times 10$ cm (L × W × D) with litter intact were randomly and carefully excavated from each subplot. The soil samples were dissected at 10 cm depth and subsequently divided into two groups: 0–5 and 5–10 cm. Within 2 days of excavation, soil samples were stored in plastic bags and transported back to an experimental greenhouse located in the South China Botanical Garden, Guangzhou, China.

Within a week of soil sampling, germination assays were conducted following the procedures described by Grime (1989). Soil samples were first passed through a 2 mm sieve to remove coarse debris. Seeds with diameter > 2 mm were returned to the soil samples. Each soil sample was spread on a layer of heat-sterilized sand (2 cm thick) in a seed germination tray. Five seed germination trays filled with sterilized sand only were used as control. All germination trays were watered daily. Newly germinated seedlings were identified, counted and then removed from the seed trays every 2 to 5 days. Unidentified seedlings were transplanted into additional germination trays for further growth for identification. The germination assay for each soil sample was concluded when no seedling emerged for 4 weeks. The mean temperature in the greenhouse was 31.5 °C and the mean relative humidity was 65.9%.

A field survey was conducted. All the above ground plant species were identified in each 5×5 m grid.

Data analysis

Seedling emergence data were converted to viable seed density (number of viable seeds per species per square meter). Data were logarithmically transformed. Differences in the number of seeds in the soil seed bank (as determined by the germination assay) between different slope locations were analysed using one way analysis of varience (ANOVA) test followed by the LSD test. Statistical analyses were performed in SPSS11.5 for Windows. Similarities between species composition in the soil seed bank and aboveground vegetation were analysed using Sorensen's community coefficient (Arroyo *et al.* 1999).

RESULTS

Seed bank density

A total of 1458 seedlings were recorded in the seedling germination assays. No seedlings emerged from the sand controls. The mean density of the shrubland soil seed bank was 1349 seeds m⁻² (Table 1). The size of the soil seed bank significantly differed with slope location (F = 7.463, p < 0.01). The base slope had the highest seed density, while the middle and upper slopes had lower but similar seed densities. Seed density was greater in the upper (0-5 cm) soil layer than in the lower (5-10 cm) layer (p < 0.05).

Seed bank species composition

The seedlings that germinated belonged to 16 species, but the life forms were limited to shrubs and herbs (Table 2). Averaged across both soil layers, the number of species detected in the seed bank ranked as follows: upper slope > middle slope = base slope. Herbaceous seeds were more abundant than shrub seeds and accounted for 63.4, 53.4 and 61.1% of the germinated seedlings in the upper, middle and base slopes respectively (Figure 2). The seed bank was typically dominated by seeds of a few species in all slope locations. For example, the seeds of two species (*Cyrtococcum patens* and *T. tomentosa*) constituted over 69% of the seed bank at the slope base and three species (Hedyotis diffusa, T. tomentosa and Mussaenda pubescens) constituted over 73.8% of the seed bank on the upper slope. No viable seeds of any tree species were recorded from the soil samples (Table 2).

Similarity between vegetation and seed bank

Many species that were conspicuous in the aboveground vegetation were absent from the seed bank and vice versa, and only five species (*T. tomentosa, M. pubescens, Melastoma sanguineum, E. lepta* and *Eurya chinensis*) were present in both the vegetation and seed bank. The similarities in species composition between soil seed bank and aboveground vegetation as expressed by the Sorensen's coefficient were low, ranging from 0.154 to 0.267 (Table 3), with the lowest at the slope base.

 Table 1
 Seed density (mean ± SE) and number of germinated seeds at different slopes

Site	Seed density (seeds m ⁻²)	Seeds germinated		
		0–5 cm	5–10 cm	Total
Upper slope	$792 \pm 167 \; b$	240	45	285
Middle slope	1347 ± 135 ab	406	81	487
Base slope	$1908 \pm 279 a$	539	147	686

Values with the same letter are not significantly different at p < 0.05.

Life form	Species	Percentage in the seed bank (%)		
		Upper slope	Middle slope	Base slope
Shrub	Mussaenda pubescens	16.12*	13.81	8.16*
	Trema tomentosa	16.78*	14.79*	17.49*
	Evodia lepta	0	9.67*	10.93
	Eurya chinensis	4.36	6.51*	0
Herb	Melastoma sanguineum	8.72*	10.85*	9.18
	Cyrtococcum patens	7.05	24.46	51.46
	Hedyotis diffusa	40.94	15.58	1.60
	Ischaemum indicum	1.01	0	0.73
	Hedyotis acutangula	0.34	3.94	0
	Eleusine indica	3.36	0	0
	Conyza bonariensis	0	0.20	0.16
	Cyperus rotundus	1.34	0	0
	Emilia sonchifolia	0.34	0	0.15
	Ludwigia hyssopifolia	0.34	0.20	0
	Commelina communis	0.34	0	0
	Ageratum conyzoides	0	0	0.15

Table 2Species composition and the percentage of each species in the seed bank at three
locations of the slope

* Indicates presence in the aboveground vegetation

 Table 3
 Similarities of species in vegetation and species in soil seed bank at different locations of slope

Location	Species in seed bank only	Species in vegetation only	Species in both vegetation and seed bank	Sorensen's coefficient
Upper slope	10	11	3	0.222
Middle slope	6	16	4	0.267
Base slope	8	14	2	0.154

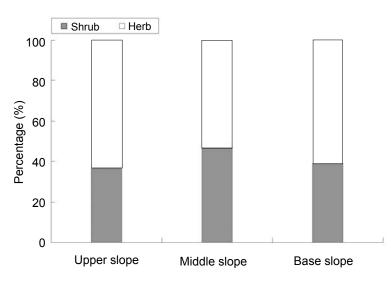


Figure 2 Seed abundance of different life forms in the soil seed bank at different locations of slope

DISCUSSION

The total seed density in this shrubland was about 1349 seeds m⁻², which is at least 20 times greater than that of pine forests, broadleaf mixed forests or broadleaf evergreen forests based on seed bank studies from the closest natural plant community, the Dinghushan Mountain Natural Reserve (Wei et al. 2005). The large seed bank size associated with the shrubland was likely the result of high seed production of shrubs and herbs, and low consumption of shrub and grass seeds by animals (Hyatt & Casper 2000, Hill & Vanderkloet 2005). Although spatial differences in shrub distribution were not investigated in this study, such differences were not obvious and we attributed the tendency of seed bank density to decline from the upper slope towards the base slope to down-slope dispersal of seeds (Arroyo et al. 1999).

In contrast to seed density, species richness in the shrubland seed bank was low compared with that of different successional stages of forest in this region because the latter have increasing numbers of tree and vine species in addition to shrubs and herbs (Wei *et al.* 2005). Other studies also indicated that, with succession, tree and vine species always increased in the seed bank while shrub and herbaceous species usually remained constant (Kalamees & Zobel 2002). Therefore, management practices to enhance conversion of shrubland to a late succession stage should increase biodiversity.

Many species represented in the aboveground vegetation were not represented in the soil seed bank even though the annual seed production of these species was plentiful. For instance, seeds of Ilex asprella and Rhodomyrtus tomentosa, the dominant species in the vegetation, were not found in the soil seed bank. Further studies are needed to understand the underlying ecological processes. Of particular importance is the absence of tree species including both pine species and indigenous broadleaf forest species. Pinus massoniana, which is native to a wide area of central and southern China, can tolerate nutrient-poor soils and low soil moisture and is a pioneer tree species in subtropical vegetation succession. The seeds of *P. massoniana*, which are 4 to 6 mm long and have a 10 to 15 mm wing, are mainly dispersed by wind after they mature in winter. When seed sources are available, this species invades bare land or shrubland and then dominates the early stages of the secondary succession and facilitates the establishment of the shade-tolerant, broadleaf evergreen tree species (Dong 1987). Since no viable seeds of *P. massoniana* were found in this shrubland soil, *P. massoniana* seedling recruitment and colonization at this particular site could be very limited.

Based on our understanding of this site, we offer three possible explanations for the absence of viable seeds of tree species in the shrubland soil seed bank: (1) Depletion of remnant tree seeds in the soil bank-this research site was deforested about 50 years ago and was then grazed or cultivated for over 20 years until it was abandoned about 20 years ago, (2) Ineffective seed dispersal -the closest natural forest is about 70 miles to the north, and seed dispersal both by wind and birds are unlikely to be very limited (Jacquemyn et al. 2003), (3) Preferential consumption of tree seeds by animals-there were a few P. massoniana trees in this shrubland, and we expected them to act as parent trees and deposit at least some seeds into the seed bank. Perhaps these seeds were produced but were consumed or killed by animals or micro-organisms.

Regarding seed predation, an experiment carried out on this site suggested that the probability of predation of tree seeds was lower when the community was dominated by grasses than by shrubs. In the earlier stages of succession, grassland community diversity was low, seed predation was not intense and seeds of P. massoniana that dispersed into the grassland-shrubland had more chances to germinate (Ren & Peng 2001, Peng 2003). As the plant community changed from grassland to shrubland, however, rodent diversity and density increased, habitats became more favourable for rodents like Bandicota indica (Peng 2003) which are major seed predators (Chung & Corlett 2006). As a result, seeds that disperse to the shrubland might be more prone to predation, therefore limiting the composition of the seed bank (Enrico et al. 2004).

Pinus massoniana is a masting species and its seed production varies greatly from year to year. This variability of annual seed production (masting effect) seems to be insignificant in the establishment of pine seedlings since our vegetation survey did not find any pine seedlings at this site. However, future studies should consider collecting soil samples at multiple years to understand the interaction of masting dynamics and seed-predator relationships. Since vegetative reproduction is an important mechanism for some broadleaf species, future studies should also consider how vegetative reproduction affects the relationship between the seed bank and aboveground vegetation in less degraded shrubland sites.

CONCLUSIONS

In the severely degraded shrubland of this study, the soil seed bank was large but its species richness was low and its composition was substantially different from that of the aboveground plant community. The secondary succession in this degraded shrubland differed from that associated with less-degraded shrublands apparently because of the absence of seeds from tree species, including pioneer trees like P. massoniana. Based on results from this study, forest management and restoration activities aimed at promoting secondary succession might need to focus on introducing seed sources (by direct planting of pioneer pine trees) rather than on increasing germination of seeds already in the seed bank. Once pine trees are established in the grassland or shrubland, the pine forest should encourage succession to a later forest stage because pine forest canopies provide a favourable understorey environment and facilitate seed dispersal by birds.

Restoration and rehabilitation of degraded ecosystems is now a global priority. Although the causes of arrested succession, and therefore the approaches needed to restore degraded fields, may vary from field to field, our results show how certain processes can block regeneration and succession. Therefore, identification of such key ecological processes may be pivotal in guiding forest management and increasing the effectiveness of restoration.

ACKNOWLEDGEMENTS

We thank our colleagues at the Heshan National Field Research Station of Forest Ecosystem and Dinghu Mountain Forest Ecosystem Station. Thanks to TT Liu, HF Lu and A Macalady for their comments. This project was supported by the National Natural Science Foundation of China (Grant No. 30670370), National Basic Research Programme of China (2009CB421101) and the Guangdong and Guangzhou Sci-Tech Planning Project (2006B60101034, 2007J1-C0471).

REFERENCES

- ARROYO MTK, CAVIERES LA, CASTOR C & HUMANA AM. 1999. Persistent soil seed bank and standing vegetation at a high alpine site in the central Chilean Andes. *Plant Ecology* 119: 126–132.
- ASHTON PMS, GAMAGE S, GUNATILLEKE IAUN & GUNATILLEKE CVS. 1997. Restoration of a Sri Lankan rain forest: using Caribbean pine *Pinus caribaea* as a nurse for establishing late successional tree species. *Journal of Applied Ecology* 34: 915–925.
- CAI XA, REN H, PENG SL & YU ZY. 1996. The productivity and biomass character study of hill slope ecosystem in Heshan. *Ecological Science* 1: 9–14.
- CHUNG KPS & CORLETT RT. 2006. Rodent diversity in a highly degraded tropical landscape: Hong Kong, South China. *Biodiversity and Conservation* 15: 4521–4532.
- COHEN S, BRAHAM R & SANCHEZ F. 2004. Seed bank viability in disturbed longleaf pine sites. *Restoration Ecology* 12: 503–515.
- DAVIES A & WAITE S. 1998. The persistence of calcareous grassland species in the soil seed bank under developing and established scrub. *Plant Ecology* 136: 27–39.
- DONG M. 1987. Population structure and dynamics of *Pinus* massoniana Lamb. on mount Jinyun, Sichuan, China. *Plant Ecology* 72: 35–44.
- ENRICO L, FUNES G & CABIDO M. 2004. Regeneration of *Polylepis* australis Bitt. in the mountains of central Argentina. Forest Ecology and Management 190: 301–309.
- GRIME JP. 1989. Seed bank in ecological perspective. In Leck MA, Parker VT & Simpson RL (Eds.) *Ecology of Soil Seed Bank*. Academic Press, San Diego.
- HAU BCH & CORLETT RT. 2003. Factors affecting the early survival and growth of native tree seedlings planted on a degraded hillside grassland in Hong Kong, China. *Restoration Ecology* 11: 483–488.
- HILL NM & VANDERKLOET SP. 2005. Longevity of experimentally buried seed in Vaccinium: relationship to climate, reproductive factors and natural seed banks. *Journal* of *Ecology* 93: 1167–1176.
- HYATT LA & CASPER BB. 2000. Seed bank formation during early secondary succession in a temperate deciduous forest. *Journal of Ecology* 88: 516–527.
- JACQUEMYN H, BUTAYE J & HERMY M. 2003. Impacts of restored patch density and distance from natural forests on colonization success. *Restoration Ecology* 11: 417–423.
- KALAMEES R & ZOBEL M. 2002. The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology* 83: 1017–1025.
- LATHAM RE. 2003. Shrubland longevity and rare plant species in the northeastern United States. *Forest Ecology and Management* 185: 21–39.
- LI ZA, ZOU B, CAO YS, REN H & LIU J. 2003. Nutrient properties of soils in typical degraded hilly land in South China. *Acta Ecological Sinica* 23: 1648–1656.

- LUZURIAGA AL, ESCUDERO A, OLANO JM & LOIDI J. 2005. Regenerative role of seed banks following an intense soil disturbance. *Acta Oecologica* 27: 57–66.
- PENG SL. 2003. Study and Application of Restoration Ecology in Tropical and Subtropical China. Science Press, Beijing.
- PUGNAIRE FI & LAZARO R. 2000. Seed bank and understorey species composition in a semi-arid environment: the effect of shrub age and rainfall. *Annals of Botany* 86: 807–813.
- REN H & PENG SL. 2001. An Introduction to Restoration Ecology. Science Press, Beijing.
- REN H, SHEN WJ, LU HF, WEN XY & JIAN SG. 2007a. Degraded ecosystems in China: status, causes, and restoration efforts. Landscape and Ecological Engineering 3: 1–13.
- REN H, LI ZA, SHEN WJ, YU ZY, PENG SL, LIAO CH, DING MM & WU JG. 2007b. Changes in biodiversity and ecosystem function during the restoration of a tropical forest in south China. *Science in China Series C* 50: 277–284.
- SATTERTHWAITE WH, HOLL KD, HAYES GF & BARBER AL. 2007. Seed banks in plant conservation: case study of Santa Cruz tarplant restoration. *Biological Conservation* 135: 57–66.

- TOH I, GILLESPIE M & LAMB D. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. *Restoration Ecology* 7: 288–297.
- WEI SJ, LI L, HUANG ZL, PENG SJ & SHI JH. 2005. Study on the dynamic of seed bank of Dinghushan forest soil. *Ecology and Environment* 14: 917–920.
- YU ZY & PENG SL. 1996. *Restoration on Degraded Ecosystems in Tropical and Subtropical China*. Guangdong Science and Technology Press, Guangzhou.
- ZHANG ZQ, SHU WS, LAN CY & WONG MH. 2001. Soil seed bank as an input of seed source in revegetation of lead/zinc mine tailings. *Restoration Ecology* 9: 378–385.
- ZIMMERMAN JK, PASCARELLA JB & AIDE TM. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* 8: 350–360.
- ZOU CB, BARRON-GAFFORD GA & BRESHEARS DD. 2007. Effects of topography and woody plant canopy cover on nearground solar radiation: relevant energy inputs for ecohydrology and hydropedology. *Geophysical Research Letters* 34: L24S21. Doi: 10.1029/2007GL031484.