Research paper

Effects of Soil Properties on Restoring Indigenous Plants in Coral Reef Landscapes

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【Summary】

Restoring indigenous plants is an urgent concern in coral reef landscapes severely invaded by white leadtrees (*Leucaena leucocephala*). The efficiency of restoration is largely influenced by the spatial heterogeneity of soils and selecting suitable species. In this study, we evaluated the relationships of soil properties with the mortality and growth performance of restored seedlings, and clarify suitable species on the basis of some specific soil properties. Seventeen species of indigenous plant seedlings were randomly planted in the study area after clearcutting white leadtrees in southern Taiwan. At the beginning of seedling planting, 142 surface soil samples were collected in a grid for analysis, including the soil depth, bulk density, water content, organic matter contents, and soil texture. Mortality and physiological characteristics of the planted seedlings, including the plant height and root collar diameter, were also investigated at 22 mo after seedling planting. Based on analytical results of a principal components analysis (PCA) and correlations, the survival rate of seedlings was determined by the soil depth, soil texture, and soil water contents in the dry season (October to April of the following year). There were significant correlation of the survival rate of seedlings with soil depth ($r = 0.58$, $p < 0.05$), sand fraction ($r = 0.63$, $p < 0.05$), and clay fraction ($r = -0.63$, $p < 0.05$). During the dry seasons, soil water contents were always below the permanent wilting coefficient, especially in clayey soils (≥ 30% clay fraction contents) in the study area. Additionally, the investigation results indicated that the growth of plants responding to soils was species specific. *Pandanus odoratissimus*, *Aglaia formosana*, *Cerbera manghas*, *Ficus superba* var.

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japonica, *Thespesia populnea*, and *Calophyllum inophyllum* were independent of soil properties and were most suitable for restoration in coastal coral reef landscapes. *Pongamia pinnata*, *Pittosporum pentandrum*, *Premna serratifolia*, *Hibiscus tiliaceus*, and *Planchonella obovata* were sensitive to soil texture and moisture stress, and should be planted in the areas with sandy soils. *Ficus septica* and *Hernanadia nymphaeifolia* were susceptible to soil depth, and these 2 species should be planted in areas with thick soil depths (≥ 30 cm). *Macaranga tanarius* and *Scaevola taccada* were species favored to grow in high-pH (≥ 7.2) areas. Furthermore, *F. benjamina*. and *Terminalia catappa* are unsuitable species for restoration of coral reef landscapes.

Key words: restoration, indigenous plant, coral reef, water stress, soil texture.

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研究報告

土壤性質對珊瑚礁地形上原生海岸林復舊之影響

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摘　要

亞熱帶或熱帶地區珊瑚礁地形上之海岸林受銀合歡(*Leucaena leucocephala*)入侵嚴重，於是原生林之復舊顯得急迫且重要。土壤性質的空間變異與復舊樹種的選擇為決定原生林復舊效率的重要因子。本研究在臺灣墾丁國家公園海岸珊瑚礁地形上，於伐除入侵之銀合歡後，種植17種臺灣海岸原生樹種，並於22個月後調查樣區內樹種存活情形、樹高與地徑；同時，以網格方式採集表土(0~15 cm)，且分析土壤基本性質(包含土壤深度、總體密度、水分含量、土壤有機質及土壤質地)，並繪製空間分布狀態。本研究之目的在於評估土壤性質與復舊樹種存活率間之關係，以及確認復舊樹種之合適性。研究主成分分析結果顯示，樹種存活率乃取決於土壤深度、質地和乾季(10月至隔年4月)時水分含量。土壤水分特性曲線結果顯示樣區土壤，於乾季時之水分含量皆低於永久凋萎點(permanent wilting coefficient)，尤其是樣區中黏粒含量高於30%之土壤，顯示植物種植於黏質地土壤中相當不易生長。此外，研究結果顯示，樹種生長情形乃取決於土壤性質之空間變異。林投、紅柴、海檬果、雀榕、欖楊與瓊崖海棠為不受樣區內土壤性質空間變異影響之樹種；存活率皆超過50%，屬於相當適合選作復舊之原生樹種。水黃皮、臺灣海桐、臭娘子、黃槿與樹青為較不耐水分逆境之樹種，需種植於樣區較砂質地之土壤中以利水分之獲取。稜果榕與蓮葉桐受土壤深度影響顯著，較適合種植於深度超過30 cm之處。血桐與草海桐較適合種植於土壤pH ≥ 7.2的區域，而白榕和欖仁為不適合於珊瑚礁地形上生長之樹種。

關鍵詞：復舊、原生樹種、珊瑚礁、水分逆境、土壤質地。

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INTRODUCTION

White leadtree (*Leucaena leucocephala* (Lam.) de Wit) is an exotic plant in Taiwan and is commonly found in subtropical and tropical coastal regions. Invasive white leadtrees rapidly form pure forests and severely damage coastal ecosystems. To sustain ecofunctions of coastal forests, regenerating coastal ecosystems by restoring indigenous plants is necessary and urgent in coastal areas underlain by coral reefs. However, the efficiency of restoring coral reef landscapes is often closely related to soil heterogeneity and plant species selected for restoration. Species-specific responses to site conditions are quite common (Sipe and Bazzaz 2001). Clear identification of the spatial heterogeneity of soil properties and selection of suitable indigenous species for restoration sites will greatly benefit the efficiency of restoration of native forests.

At the beginning of restoration, establishing seedlings is most critically influenced by environmental conditions (Walters and Reich 2000). Soil functions are considered critical factors in determining the growth of plants, including soil pH, water availability, organic matter, and soil texture (Schaff et al. 2003, Hartman and McCarthy 2004, Hopmans et al. 2005, Pezeshki et al. 2007). Johnston and Crossley (2002) stated that it is crucial to identify soil functions that must be preserved in forest systems, such as the hydrology, physical characteristics, and nutrient cycles. Among soil properties, the soil water content is the most critical factor for determining the survival or growth of restored plants. Verdaguer et al. (2011) found that one of the main constraints on reforestation is low water availability during the first year after the planting of seedlings. Low soil moisture is critical for seedling recruitment and a primary reason for seedling mortality (Lamont et al. 1993, Lauenroth et al. 1994). Moreover, soil depth and soil texture are most often used as alternative variables for water availability in plants, because soil texture limits water availability in soils, especially during drought periods (Grossnickle 2005, Padilla and Pugnaire 2007). Sher and Marshall (2003) reported that growth conditions and mortality of newly recruited cottonwood seedlings are influenced by the soil texture, which affected both water drainage rates and the extent of capillary rise during initial establishment years in New Mexico, USA. Bhattacharjee et al. (2008) also indicated that seedlings might experience greater moisture stress in loamy or clayey soils than in sandy soils, and high mortality of seedlings could be found in loamy or clayey soils. Except for moisture regimes in clayey soils, the growth of seedling roots might be mechanically impeded, further resulting in the death of seedlings (Clark et al. 2003). Pezeshki et al. (2007) also indicated that restored black willow (*Salix nigra*) cuttings grew more effectively in sandy soils than in loamy soils because of expansive development space for roots in a streambank during a restoration practice in Mississippi, USA.

Soil pH and organic matter are also critical factors affecting the growth of plants during restoration or reforestation. Hartman and McCarthy (2004) stated that soil pH influenced the growth of *Lonicera maackii* during a restoration process in an abandoned factory in Ohio, USA. In addition, soil organic matter significantly contributes to physical, chemical, hydrological, and biological soil properties, and these life-supporting processes are largely regulated by biological soil activity (Setälä et al. 2000, Hopmans et al. 2005, Chang et al. 2011).

Southern Taiwan contains over 9000 ha of coastal areas consisting of middle-late Pleistocene uplifted reefs. These coastal coral reef landscapes are characterized by shallow soils, high soil pH, and low water retention capacity, and many areas have already been largely invaded by white leadtrees (Lu and Chung 2007). To regenerate biodiversity and produce sustainable ecosystems, clearcutting of invasive white leadtrees following restoration of indigenous plants has been strongly recommended in coastal areas of southern Taiwan (Wang and Hung 2005). Concurrently, the poor soil quality of these coastal areas was also considered to limit the growth of restored plants, especially during the initial restoration period. In the present study, we hypothesized that the unrealized spatial heterogeneity of soil properties in coral reef landscapes, and selection of unsuitable indigenous plant species could substantially limit the performance of restoration. Therefore, this study aimed to: (1) determine correlations of soil properties with survival rates and growing performances of planted indigenous seedlings; and (2) find suitable species for coastal forest restoration, based on the spatial heterogeneity of soil properties by a field practice of restoration.

MATERIALS AND METHOIDS

Environmental setting of the study area

This study was conducted on a raised coral reef terrace (approximately 120°42.0'E; 21°59.9'N) in Kenting National Park (KNP), southern Taiwan (Fig. 1). The area of the study site is approximately 2.2 ha (80 m wide and 280 m long). The climate of the study area is characterized by high temperatures and a long dry season (from October to April of the following year). The mean annual temperature is 26℃, with an average range

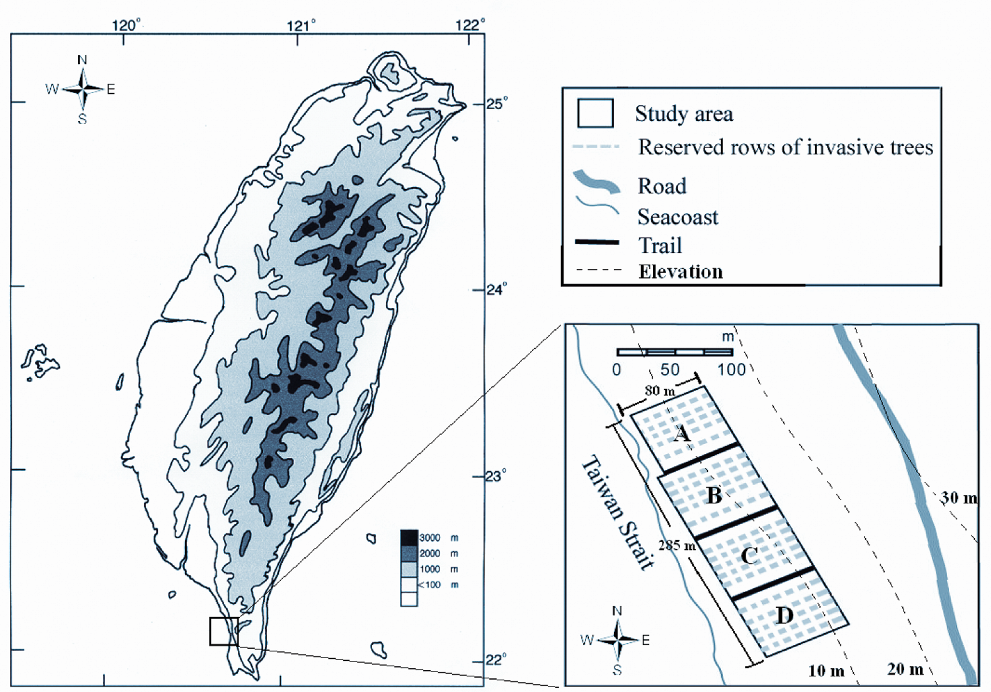

Fig. 1. Location of the study area.

of 28℃ in July to 18℃ in January. The annual rainfall, ranging 1800~2400 mm, largely falls from May to September (the wet season) (Central Weather Bureau 2010). The soil moisture regime is udic, whereas the soil temperature regime is hyperthermic. The study soils were classified as Udipsamment and Dystrudepts, based on US Soil Taxonomy (Soil Survey Staff 2010). In southern Taiwan, at least 48% of forests, including coastal forests, have been largely invaded by white leadtrees (Chin et al. 2007, Lu and Chung 2007).

Clearcutting of white leadtrees

Before clear felling of the invasive white leadtrees at the study site, the stand density of trees with a diameter at breast height (DBH) exceeding 1 cm was 7645 trees ha^{-1}, with a basal area of 18.4 m^2 ha^{-1}. Before clear felling, the stand density of white leadtrees was 5504 trees ha^{-1} (approximately 75% of the stand), with a basal area of 8.6 m^2 ha^{-1}. In addition, the stand was also dominated by *Broussonetia papyrifera* (L.) L'Herit. ex Vent., *Melanolepis multiglandulosa* (Reinw.) Reich. f. &Zoll., *Macaranga tanarius* (L.) Muell.-Arg., *Ehretia dicksonii* Hance, and *Ehretia resinosa* Hance before clear felling.

The clear felling of invasive white leadtrees was conducted in May 2008. Twenty-six rows of white leadtrees were preserved to provide shade to facilitate the growth of restored seedlings in the study area. Seedlings of 17 indigenous species were planted in June 2008, and the planted density was approximately 1530 trees ha^{-1}. A field investigation, involving survival and the size (height and root collar diameter) of the planted indigenous trees, was also conducted 22 mo after the seedlings were planted in April 2010. The study area was divided into 4 sub-blocks (replications) (Fig. 1), and the survival and size were investigated in 3 small plots (30 × 30 m) randomly selected in each sub-block. In addition, the sturdiness quotient (SQ) was also calculated, based on the plant height and root collar diameter. The SQ is the ratio of height (cm) to root collar diameter (mm). Seedlings with a higher SQ tend to be more susceptible to damage from wind and drought (Roller 1977), whereas a lower ratio suggests a stouter seedling (Haase 2007, Bayala et al. 2009). The lower the quotient that is measured, the higher the perceived seedling quality is.

Field procedures and laboratory analyses of soil

Soil samples were systematically collected using a grid method in May 2010. A 15 × 15-m grid sampling was conducted, and 142 surface soil samples were collected for physical and chemical analyses. Soil depth was determined using a spiral auger by drilling to the parent material (coral reefs) at each sampling point. The auger has a 38-mm-diameter × 102-mm-long auger bit, with a total length of 915 mm. Nearby the drilled hole for soil depth determination, 2 stainless steel cores (50-mm inner diameter × 60-mm height) were used to determine the bulk density (Db) of the surface soil (Blake and Hartge 1986). Approximately 200 g of soil (0~15 cm) was also collected for further soil analyses including pH, soil water content, texture, and soil organic carbon (SOC) content. Soil water contents were determined using a gravimetric method. The particle size distribution was determined using the pipette method (Gee and Bauder 1986). Moreover, the pH values of air-dried samples (< 2 mm) was determined in a mixture of soil and deionized water using a glass electrode (McLean 1982). Finally, the SOC content was determined using the Walkley-Black wet oxidation method (Nelson and Sommers 1982). A pressure plate extractor (Soil Moisture, SB, CA, USA) was used to determine the water retention curve of the study soils (Klute 1986). This study estimated soil volumetric water contents at different matric pressures, including 0, 517, 1034, 2068, 4134, 6202, 8269, and 11,370 cm.

Statistical analyses

All data were analyzed using SPSS12.0 for Windows software (SPSS, Chicago, IL, USA). A one-way analysis of variance (ANOVA) and post-hoc comparison tests were performed using soil properties of each sub-block divided by spatial parameters. Differences between mean values were identified using Duncan's test. Pearson correlation coefficients were calculated to examine how the soil properties were related. Data were also subjected to a principal components analysis (PCA) using a varimax-rotated factor matrix to obtain a matrix. In this study, all principal factors extracted from the variables with eigenvalues of ≥ 1.0 were retained as suggested using the Kaiser criterion (Kaiser 1960). Factor loadings of ≥ 0.60 are typically regarded as strong (García et al. 2004).

RESULTS AND DISCUSSION

Soil characteristics and spatial distribution

Table 1 lists the soil properties. The studied soils were shallow with a low mean bulk density (Db) (1.0 Mg m^{-3}). Low soil water contents (2.3~23%) were found during the dry season (from October to April), and

Table 1. Characteristics of soils and indigenous plants in the 4 sub-blocks in the study area

Characteristics of soils and indigenous plants	A (*n* = 36)	B (*n* = 36)	C (*n* = 35)	D (*n* = 35)
Depth (cm)	32 ± 12a	25 ± 11b	19 ± 12c	16 ± 9.8c
Bulk density (Mg m^{-3})	1.0 ± 0.3a	0.9 ± 0.2ab	1.0 ± 0.1ab	1.0 ± 0.1b
Water content in the dry season (w/w, %)[a]	7.9 ± 2.4a	6.8 ± 3.3a	8.0 ± 3.4a	7.2 ± 0.3a
Water content in the wet season (w/w, %)[b]	30 ± 9.3a	29 ± 7.5a	29 ± 4.8a	39 ± 7.7b
pH	7.1 ± 0.1a	6.9 ± 0.2b	6.9 ± 0.2b	7.2 ± 0.3c
Organic carbon content (%)	2.7 ± 0.8a	3.3 ± 1.1b	4.5 ± 1.4c	3.6 ± 1.5b
Sand (%)	52 ± 13a	45 ± 17ab	37 ± 15c	41 ± 16bc
Silt (%)	28 ± 8.1a	29 ± 11ab	32 ± 9.2b	31 ± 10b
Clay (%)	20 ± 6.5a	26 ± 8.8ab	31 ± 8.0c	28 ± 9.0bc
Representative soil texture	SL	SCL	CL	L
Permanent wilting coefficient (%)[c]	4.92	11.8	18.6	15.1
Survival rates of seedlings (%)	63	52	44	50
Sturdiness quotient (SQ)	6.23 ± 1.11a	6.66 ± 1.78a	5.79 ± 1.32a	6.79 ± 2.31a

[a] The duration of the dry season was October to April.

[b] The duration of the wet season is May to September.

[c] Obtained from the water retention curve.

Values followed by the same latter within the same row do not significantly differ at the 5% level.

SL, sandy loam; SCL, sandy clay loam; CL, clay loam; L, loamy.

11~49% of the soil water contents were found during the wet season (from May to September). The soils were characterized as being neutral to slightly alkaline. The mean SOC content was approximately 3.6%. As the for soil particle size distribution, a wide range of textures was found, ranging from sandy loam to silty clay. Respective contents of sand, silt, and clay fractions were 44, 29, and 27% on average. A spatial analysis based on a Kriging interpolated estimation displayed the heterogeneous spatial distribution of soil properties in the entire study area. The soil depth, bulk density, and sand fraction gradually decreased from north to south in the study area. However, soil pH, water contents, SOC contents, and the fractions of silt and clay increased from north to south (Fig. 2). From sub-block A to sub-block D, the soil depth significantly decreased ($p < 0.05$) (Table 1). No differences in water contents were apparent between each sub-block in the dry or wet season, except for the soil in sub-block D in the wet season. The highest SOC content was found in sub-block C, and the lowest was in sub-block A. Fractions of sand, silt, and clay in sub-blocks A and B seemed to significantly differ from those in sub-blocks C and D. Soils in sub-block A were sandier than in other sub-blocks, and soils in sub-block C were more clayey than in other sub-blocks.

Variable soil properties are usually found in floodplains (Eckstein and Donath 2005, Bhattacharjee et al. 2008) and coastal areas

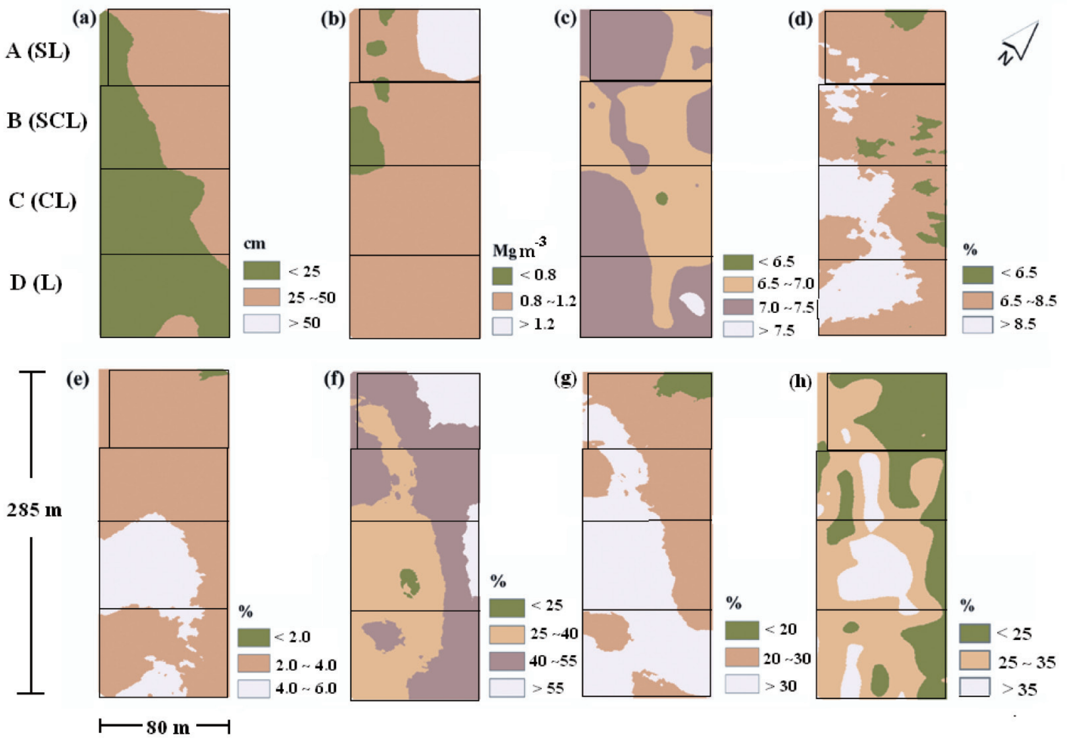

Fig. 2. Spatial distributions of soil properties in the study area: (a) soil depth; (b) bulk density; (c) soil pH; (d) soil water in dry season; (e) organic matter; (f) sand fraction; (g) silt fraction; and (h) clay fraction. The black solid frames represent different sub-blocks.

(Walmsley and Davy, 1997) where there are frequent natural disturbances, such as periodic flooding. The spatial heterogeneity of soil properties, including soil depth or moisture stress resulting from the soil texture, was confirmed to lead to a poor efficiency of restoration of native trees in these areas.

Survival rate and sturdiness ratio of indigenous seedlings

Survival rates of restored seedlings in the 4 sub-blocks were 63, 52, 44, and 51% in sub-blocks A, B, C, and D, respectively (Table 1). The lowest survival rate of restored seedlings was found in sub-block C. Most of the species we restored grew effectively in sub-block A; however, only 6 of 17 species of planted indigenous trees revealed a high survival rate (≥ 50%) in sub-block C (Table 2), indicating in that some soil properties were unsuitable for growing vegetation in that sub-block. Table 2 also shows that *F. benjamina* L. and *Terminalia catappa* L. performed lowest in all sub-blocks, indicating that these 2 species are unsuitable for restoration in our study area. Nevertheless, *Pandanus odoratissimus* Linn.f., *Aglaia formosana* (Hayata) Hayata, *Cerbera manghas* L., *F. superba* (Miq.) Miq. var. *japonica* Miq., *Thespesia populnea* (L.) Solad ex Correa, and *Calophyllum inophyl-*

Table 2. Survival rates of indigenous seedlings in the 4 sub-blocks in the study area

Plant species	A	B	C	D
Pongamia pinnata (L.) Pierre ex Merr.	0.88 (25)	0.79 (28)	**0.42 (26)**	**0.40 (25)**
Pittosporum pentandrum (Blanco) Merr.	0.91 (22)	0.90 (20)	**0.45 (33)**	0.90 (21)
Ficus benjamina L.	**0.24 (17)**	**0.23 (22)**	**0.29 (17)**	**0.33 (21)**
Macaranga tanarius	**0.38 (50)**	**0.31 (49)**	**0.45 (62)**	0.65 (55)
Pandanus odoratissimus Linn. f.	1.00 (15)	0.62 (26)	0.71 (26)	0.82 (22)
Aglaia formosana (Hayata) Hayata	0.90 (20)	0.94 (17)	0.50 (24)	0.89 (18)
Cerbera manghas L.	0.82 (17)	0.82 (17)	0.74 (23)	0.73 (22)
Premna serratifolia L.	0.60 (20)	0.58 (26)	**0.25 (24)**	0.52 (23)
Scaevola taccada (Gaertner) Roxb.	**0.11 (18)**	**0.08 (24)**	**0.32 (25)**	0.59 (27)
Ficus Superba (Miq.) Miq. var. *Japonica* Miq.	0.88 (17)	0.67 (21)	0.65 (23)	0.87 (23)
Hibiscus tiliaceus	0.62 (66)	0.52 (75)	**0.38 (71)**	**0.39 (77)**
Ficus septica Burm. f.	0.74 (61)	**0.44 (68)**	**0.27 (77)**	**0.32 (81)**
Hernanadia nymphaeifolia (Presl) Kubitzki	0.58 (12)	**0.40 (20)**	**0.12 (27)**	**0.38 (13)**
Planchonella obovata (R. Br.) Pierre	0.82 (11)	0.77 (22)	**0.35 (17)**	0.85 (20)
Thespesia populnea (L.) Solad ex Correa	0.90 (49)	0.73 (51)	0.91 (55)	0.79 (42)
Calophyllum inophyllum L.	0.88 (16)	0.52 (27)	0.52 (27)	0.88 (24)
Terminalia catappa L.	**0.35 (69)**	**0.39 (83)**	**0.34 (87)**	**0.16 (77)**
Total numbers of planted indigenous seedling in each sub-block	**517**	**603**	**656**	**610**

Values in parentheses indicate the investigated numbers of seedling.
Values in bold indicate a survival rate of < 50%.

Table 3. Correlation coefficients between soil properties and survival rates of indigenous seedlings in all 4 sub-blocks in this study (n = 12)

	Depth	Db	WC(d)	WC(w)	pH	SOC	Sand	Silt	Clay	SR
Depth	1.00									
Db	0.59*	1.00								
WC(d)	-5.00	0.14	1.00							
WC(w)	-0.20	-0.03	0.23	1.00						
pH	-0.15	0.01	0.41	0.59*	1.00					
SOC	-0.81**	-0.47	0.31	0.10	-0.13	1.00				
Sand	0.92**	0.54*	-0.43	-0.07	0.03	-0.96**	1.00			
Silt	-0.71**	-0.67*	0.12	-0.21	-0.29	0.89**	-0.89**	1.00		
Clay	-0.94**	-0.37	0.65*	0.26	0.21	0.84**	-0.93**	0.67*	1.00	
SR	0.58*	0.12	-0.14	-0.44	0.09	-0.71**	0.63*	-0.45	-0.63*	1.00

* $p< 0.05$; ** $p< 0.01$; Db, bulk density; WC(w), water content in wet season; WC(d), water content in dry season; OC, organic carbon content. SR, survival rate.

lum L. revealed relatively high survival rates. High mortalities were found for *Pongamia pinnata* (L.) Pierre ex Merr., *Pittosporum pentandrum* (Blanco) Merr., *Premna serratifolia*, *Hibiscus tiliaceus*, and *Planchonella obovata* (R. Br.) in sub-blocks C and D. Regarding the substrate of restored trees, some soil properties distributed in sub-blocks C and D differed from those in sub-blocks A and B and were vital factors leading to high mortality of some species of restored trees, including depth, water content, organic matter, and soil texture (Fig. 2). After 22 mo, residual live seedlings in each sub-block seemed to be growing effectively, irrespective of the soil properties. However, surviving seedlings in sub-block C seemed to have larger root systems (low sturdiness quotient) than those in other sub-blocks, implying that seedlings in sub-block C had more difficulty obtaining water or nutrients from soils, and therefore, had developed large root systems (Bayala et al. 2009). Our results also corresponded with those of Li et al. (2008) who found that moisture stress resulted in high ratios of root mass to stem mass of restored plants, implying that large root systems develop in wate-deficient soils in order to obtain more available water.

Relationships between soil properties and survival rates of indigenous seedlings

Based on the investigated results of the survival rates of seedlings from 12 experimental small plots (30 × 30 m), survival rates of seedlings of indigenous trees had significantly positive correlations with soil depth (r = 0.58*) and the sand fraction content (r = 0.63*) (Table 3). This suggests that the roots of seedlings can easily extend and obtain more water and nutrients from deeper and coarser textural soils (Friedman et al. 1995, Sher and Marshall 2003), because those soils have more interstitial spaces and larger voids than do clayey soils. Bhattacharjee et al. (2008) also indicated that sites with coarser soils may be more suitable for restoration than finer soils, because coarser soils not only supply higher-quality growing media but are also associated with lower herbaceous vegetation, thereby reducing shading effects. However, significant negative correlations between the survival rate of seedlings and the SOC (r = -0.78**) and clay fraction content (r = -0.63*) were found. Bhattacharjee et al. (2008) also revealed that seedlings of a restored cottonwood experienced greater moisture stress in loamy and clayey soils than in sandy soils. Soil texture influences both soil drainage and the extent of capillary rise, limiting the available water for seedlings (Mahoney and Rood, 1991).

To examine the relationships between soil properties and survival rates of seedlings more closely, a PCA was performed. The PCA results further verified the critical soil properties that determined the survival of seedlings. Three groups were clearly separated based on the PCA, which totally explained 84.7% of the total variance. The first component (PC1), which accounted for 51.1% of the variance, could be interpreted as growth performance-influencing factors, and was dominated by soil depth, Db, soil water contents in dry season (WC(d)), SOC, soil texture, and survival rates of seedlings (Fig. 3). Based on loadings of various properties on PC1, the soil depth, Db, and sand fraction content were clearly positively correlated with the seedling survival rate, implying that a greater soil depth and sand fraction increased to the seedling survival rate. In addition, negative feedback from the SOC, WC(d), and the contents of silt and clay fractions was harmful to seedlings. The second component (PC2), included pH and WC(w) and accounted for 17.2% of the variance, which is considered a possible salinity factor. The third component (PC3), explained approximately 16.4% of the variance, and included WC(d) and the content

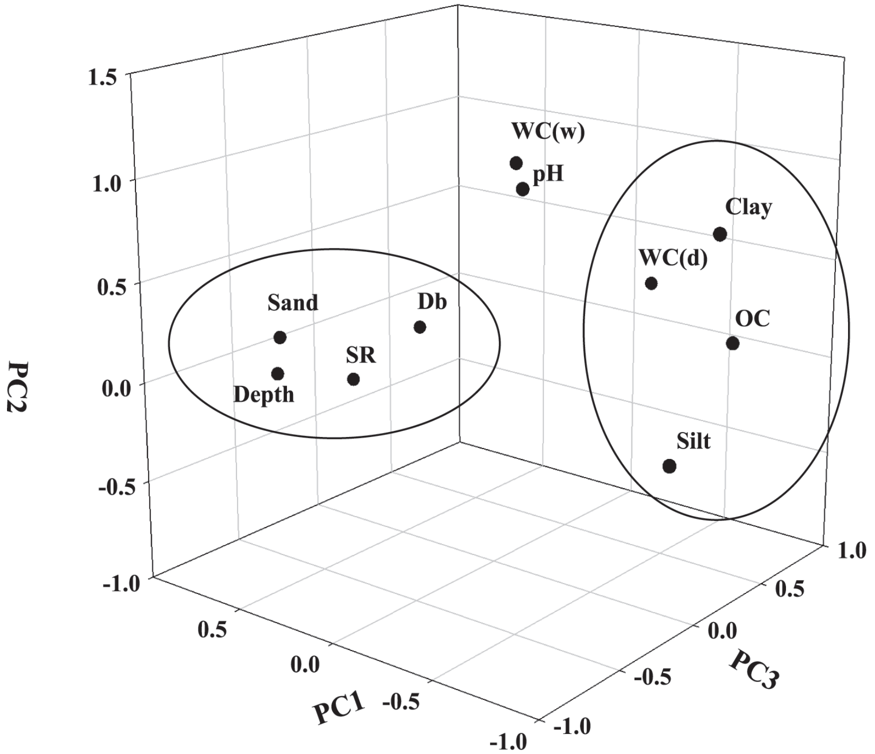

Fig. 3. Principle component (PC) analysis of soil properties and survival rates (SRs) in this study (*n* = 12). Db, bulk density; WC(w), water content in wet season; WC(d), water content in dry season; OC, organic carbon content.

clay fraction; it was considered a water availability factor. High (≥ 0.50) and positive loadings of WC(d) and clay on PC3 indicated that soil moisture in the dry season was influenced by the clay fraction content in our study area. Sprenger et al. (2002) observed that the soil texture affected the germination and growth of cottonwood, especially in soils consisting of > 65% clay which obviously reduced its germination. Bhattacharjee et al. (2008) also indicated that finer soils (loam or silt loam soils) experienced greater moisture stress than coarser ones (sandy loam soils), and this was the major reason for the high mortality of restored seedlings.

According to the results of the ANOVA (Table 1) and PCA (Fig. 3), a thin soil depth and water deficiency in the dry season might be critical factors causing death of the seedlings, whereas the soil moisture in the dry season was mainly determined by the SOC and contents of silt and clay fractions, particularly the clay content. Therefore, to evaluate the soil water availability in the dry season, permanent wilting coefficients of the soils with 4 typical textures in this study area were determined, based on the water retention curves (Fig. 4). Soils in sub-blocks C and D were characterized by higher values of the permanent wilting coefficient than were soils in sub-blocks A and B. Additionally, Fig. 4 shows that a higher rate of moisture decline was discovered in sandy soils than in clayey soils, and the water-retention capacity was larger in clay soils than in sandy soils, reflecting that plants have greater difficulty obtaining available water from clayey soils. In this study, water contents in the dry season were

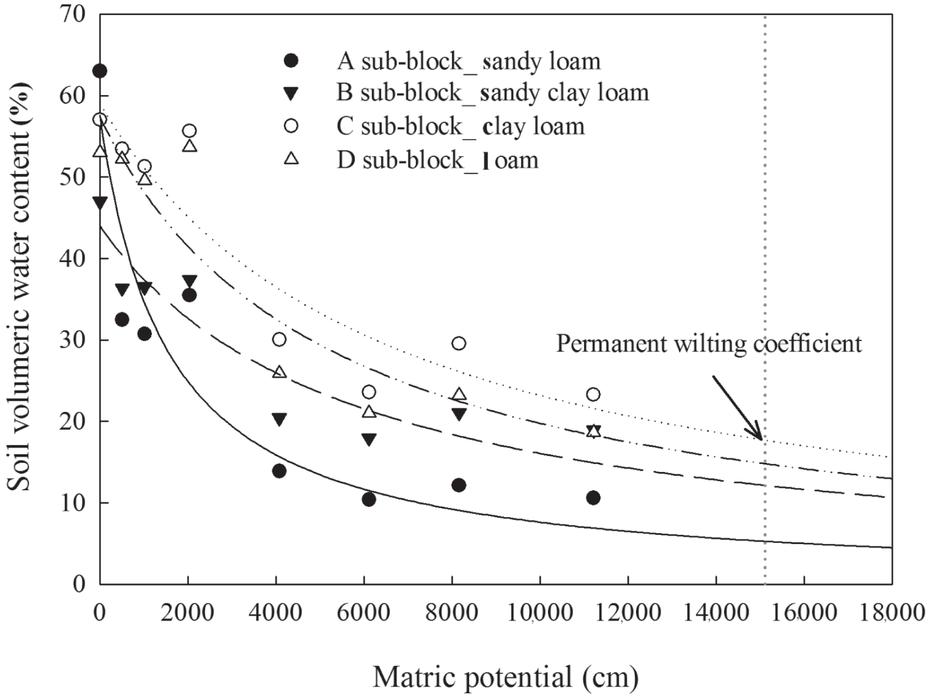

Fig. 4. Water retention curves of 4 dominant soil textures in the study area. The dotted line marked at 15,510 cm indicates the permanent wilting coefficient for each sub-block.

relatively low, and never exceeded the permanent wilting coefficient in sub-blocks C and D (Table 1). This indicates that obvious water stress existed for seedlings in sub-blocks C and D, where high mortality (≥ 50%) of seedlings was revealed in this study. Structural limitations of seedlings usually occur in soils with water stress and a thin depth, which could also explain the high mortality (Verdaguer et al., 2011). Eckstein and Donath (2005) and Verdaguer et al. (2011) also indicated that a water deficiency in growing media is a major factor retarding seedling development and increasing mortality of restored seedlings.

Effects of soil properties on the performance of residual live seedlings

Because of the homogenous planting density of seedlings (2 m between each seedling) and shading (the seedlings were planted equidistantly along rows between preserved rows of white leadtrees), the effects of competition of plants and shading on the growth of seedlings might have been diminished. Therefore, differences in the growth of seedlings were considered to have resulted from soil heterogeneity. The SQ of every residual live seedling after 22 mo was calculated based on the seedling height and root collar diameter in each sub-block. Evaluating the growth performances of seedlings among plant species by SQ comparisons is difficult because the ability for photosynthesis relatively differs among plant species. However, for a given species, the differences of growing performance of seedlings in different sub-blocks could be compared according to the SQ to evaluate the influences of soil properties on growing conditions.

Table 4 shows that the growth of seedlings seemed to depend on soil properties after the seedlings were planted, and the influence was species-specific. No significant differences in the SQ of residual live seedlings were found in 11 of 17 species among the 4 sub-blocks. Moreover, in contrast to Table 1, *Pittosporum pentandrum* and *Premna serratifolia* might have presented higher seedling quality in finer soils with a thin depth and higher pH levels. The residued live seedlings of these 2 species might have resisted enviromental stresses due to their physiological characteritics like improved photosynthesis, stomatal conductance, and transpiration rates (Verdaguer et al. 2011).

In contrast, *Scaevola taccada* (Gaertner) Roxb., *Hibiscus tiliaceus*, and *Hernanadia nymphaeifolia* (Presl) Kubitzki seemed to have lower performances when planted in soils with a pH of ≥ 7.2, which also agrees with Lan (2011).

Implications for the restoration of coastal forests in Taiwan

In our study, seedlings were randomly planted in each sub-block with an identity density based on a random complete block design (RCBD). Therefore, plant species and heterogeneous soil characteristics were 2 major parameters in this study determining the success of restoring indigenous plants. Carefully selecting restored plant species and planting in suitable soil environments substantially facilitated efficient restoration.

Based on our results, low mortality rates (≤ 50%) were found for *Pandanus odoratissimus*, *Aglaia formosana*, *Cerbera manghas*, *F. superba* var. *japonica*, *Thespesia populnea*, and *Calophyllum inophyllum* in all sub-blocks, and these 6 species could be considered the most suitable plants for restoration in coral reef landscapes. Additionally, at 22 mo after the seedlings were planted, morphological characteristics of each of the 6 species also showed no significant differences among the 4 sub-blocks (Table 4), further reflecting that the growth performances of these 6 spe-

Table 4. Sturdiness quotient (SQ) of each indigenous plant species in the 4 sub-blocks (A-D) of the study area

Plant species	A	B	C	D
Pongamia pinnata (L.) Pierre ex Merr.	6.78 ± 2.12a	6.44 ± 1.90a	6.92 ± 2.37a	5.89 ± 2.12a
Pittosporum pentandrum (Blanco) Merr.	6.99 ± 1.97a	5.81 ± 2.07a	5.98 ± 1.82a	5.79 ± 1.79b
Ficus benjamina L.	5.37 ± 2.30a	4.93 ± 1.41a	6.16 ± 1.15a	5.23 ± 1.69a
Macaranga tanarius	5.63 ± 2.11a	6.13 ± 1.77a	5.25 ± 1.63a	6.5 ± 4.11a
Pandanus odoratissimus Linn. f.	3.27 ± 2.04a	2.36 ± 0.59a	3.55 ± 3.89a	4.08 ± 2.26a
Aglaia formosana (Hayata) Hayata	7.74 ± 4.25a	6.68 ± 1.79a	7.13 ± 1.25a	7.14 ± 2.60a
Cerbera manghas L.	5.14 ± 1.14a	5.26 ± 1.52a	5.41 ± 2.68a	5.04 ± 1.40a
Premna serratifolia L.	9.45 ± 3.98a	8.69 ± 2.66a	6.75 ± 2.97b	5.86 ± 2.45b
Scaevola taccada (Gaertner) Roxb.	3 ± 0.90a	3.13 ± 1.09a	3.15 ± 1.73a	4.78 ± 2.42b
Ficus Superba (Miq.) Miq. var. *Japonica* Miq.	8.2 ± 3.39a	6.18 ± 2.10a	7.09 ± 1.64a	7.58 ± 2.36a
Hibiscus tiliaceus	5.19 ± 3.37a	5.94 ± 2.13ab	5.67 ± 1.84ab	6.66 ± 3.02c
Ficus septica Burm. f.	5.65 ± 1.98a	5.82 ± 1.98a	5.96 ± 1.02a	6.47 ± 2.81a
Hernanadia nymphaeifolia (Presl) Kubitzki	4.73 ± 1.85a	4.84 ± 1.13a	4.84 ± 0.80a	6.15 ± 1.80b
Planchonella obovata (R. Br.) Pierre	7.73 ± 3.39a	8.06 ± 2.66a	8.86 ± 2.11a	8.41 ± 2.94a
Thespesia populnea (L.) Solad ex Correa	6.66 ± 2.34ab	7.06 ± 3.78b	5.85 ± 1.97c	7.32 ± 3.19b
Calophyllum inophyllum L.	6.46 ± 2.87a	5.55 ± 1.44a	5.56 ± 1.18a	6.56 ± 2.42a
Terminalia catappa L.	5.59 ± 2.80a	6.34 ± 1.91a	5.79 ± 5.44a	5.41 ± 1.94a

Values followed by the same latter within the same row do not significantly differ at the 5% level.

cies were independent of soil properties in the study area. Conversely, high mortalities (≥ 50%) were found for *F. benjamina* and *Terminalia catappa* in all sub-blocks, suggesting that these 2 species were relatively unsuitable for restoration in coral reef landscapes. However, the death of *Terminalia catappa* might not have been related to soil properties, but resulted from animal damage in the dry season (Wang et al. 2009).

Excluding the aforementioned 8 plant species, the growth of other species seemed to be influenced by soil properties. *Macaranga tanarius* and *Scaevola taccada* were found to grow effectively in sub-block D where the soils had significantly higher pH levels and WC(w) than in other sub-blocks. Based on the PCA results, WC(w) was not a major factor determining survival rates of our restored plants; therefore, we considered that *Macaranga tanarius* and *Scaevola taccada* were species suitable for growing in areas with high pH (≥ 7.2). (Chen and Horng 1993). Aside from the pH, soil depth might be a factor influencing plant growth, such as the species of *F. septica* and *Hernanadia nymphaeifolia* which only grew well in sub-block A which had a significantly thicker depth of soils, reflecting that the growth conditions of these 2 species may be susceptible to soil depth. Table 4 also demonstrates that *F. septica* and *Hernanadia nymphaeifolia* were more robust in sub-block A than in those that grew in the other 3 sub-blocks, although no obvious differences in SQ were found among the 4 sub-blocks.

The remaining 5 species, *Pongamia pinnata* (L.) Pierre ex Merr., *Pittosporum pentandrum* (Blanco) Merr., *Premna serratifolia* L., *Hibiscus tiliaceus*, and *Planchonella obovata* (R. Br.) Pierre, were sensitive to clay contents that determine water availability in the dry season, because these 5 species showed high mortality in sub-blocks C and D, especially the species *Pittosporum pentandrum*, *Premna serratifolia*, and *Planchonella obovata*. During the dry season, available water was deficient and almost below the permanent wilting coefficient in soils of sub-blocks C and D, indicating that available water was tightly adsorbed onto soil particles, possibly leading to the wilting of seedlings. This finding also suggests that water stress was more serious for residual live seedlings in loamy and clayey soils during the dry season in this study.

CONCLUSIONS

A clear understanding of the spatial heterogeneity of soil properties and careful selection of plant species suitable for specific soil properties can substantially benefit restoration efficiency. Our results indicated that soil depth, soil water contents in the dry season, and soil texture were crucial factors determining the survival rate and growth performance of seedlings during restoration processes. Coarser or deeper soils may reveal higher restoration efficiencies than finer soils. The results showed that the growing conditions of *Pandanus odoratissimus*, *Aglaia formosana*, *Cerbera manghas*, *F. superba* var. *japonica*, *Thespesia populnea*, and *Calophyllum inophyllum* were independent of soil properties and were most suitable for restoration in coastal coral reef landscapes. *Pongamia pinnata*, *Pittosporum pentandrum*, *Premna serratifolia*, *Hibiscus tiliaceus*, and *Planchonella obovata* were sensitive to soil texture. Moisture stress caused from clayey soils in the dry season led to high mortality of these 5 species. *Ficus septica* and *Hernanadia nymphaeifolia* were susceptible to soil depth, and these 2 species should be planted in areas with thick soil depths. *Macaranga tanarius* and *Scaevola taccada* grew well in high-pH (≥ 7.2) areas. Furthermore, *F. benjamina* and *Terminalia catappa* were unsuitable species for restoration of coastal coral reef landscapes.

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