



The influence of gap creation on the regeneration of *Pinus tabuliformis* planted forest and its role in the near-natural cultivation strategy for planted forest management

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ABSTRACT

It remains unclear whether or not creating gaps in planted forests can increase the plant species composition, structure, and biodiversity, and also whether it can be helpful for restoring planted forests (to a more natural state). Based on a comparison of species composition and structure among forest patches, small gaps (4–25 m²), medium gaps (25–150 m²) and large gaps (150–450 m²), we found that (1) creating gaps enhanced vascular plant diversity. Both the species richness and Shannon diversity indices of small, medium and large gaps were significantly higher than in the understory. The pattern of increasing diversity of vascular plants with gap creation could be partly attributed to the emergence of novel shade intolerant species in gaps. (2) Creating gaps favored the colonization and regeneration of native species. Gap size influenced not only the emergence and density of individuals of different species, but also the emergence of different life form types. Small gaps promoted the regeneration of some shrub species, such as *Ostryopsis davidiana*, *Rosa hugonis*, and *Forsythia suspense*, leading to these species becoming canopy dominants early on in succession. The medium and large gaps favored the growth of tree species, such as *Populus davidiana* and *Betula platyphylla* (early successional stage), and *Quercus liaotungensis* and *Pinus tabulaeformis* (later successional phase). (3) The canonical correspondence analysis showed that plant species composition and distribution were mainly influenced by gap size and slope aspect, and that the recorded plant species could be divided into three life forms (trees, shrubs and herbs) on the biplot diagram. (4) Finally, creating gaps provided opportunities not only for native pioneer species in the early successional stage, but also for climatic climax species to grow to canopy dominants in later successional phases, suggesting that a more natural forest will develop with plant succession. Gap size plays an important role in plant regeneration, and it could be used to produce desired successional communities in near natural management for planted forests.

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1. Background

To meet new silvicultural, ecological and social management objectives, silvicultural systems must evolve beyond their traditional emphasis on timber production to include the broader objectives of protecting sensitive species, sustaining ecosystem functions (diversity, productivity, nutrient cycling and resilience) and identifying sustainable levels of use for a broad range of renewable resources (Nakamura et al., 2005; Coates and Burton, 1997). For a long time, creating gaps has become a focus of managers attempting to emulate natural disturbance regimes and to improve the composition, structure and biodiversity of vascular plants in planted forests (Hartshorn, 1989; Attiwill, 1994; Roberts

and Gilliam, 1995; Fahey and Puettmann, 2008). However, most of the research to date has focused on natural forests and only a few studies have considered planted forests (Nakamura et al., 2005). Hence, it remains unclear whether or not creating gaps could be successful for planted forest regeneration. To address this issue, we considered the following 3 questions: (1) does gap creation influence plant species diversity in artificial forest? (2) are different plant species differentially affected by gap size? and (3) does gap creation favor colonization by native species?

Several studies (Ricklefs, 1977; Connell, 1978; Van Der Meer et al., 1999) have found that gaps can enhance the plant species diversity of forest ecosystems because they provide openings for non-shade-tolerant species and pioneer species. Conversely, Hubbell et al. (1999) found that while gaps increased seedling establishment and sapling densities in a tropical forest, they did not increase the tree species diversity in the long-term. A transient increase in species diversity was observed after gap

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creation, but this effect dissipated as self-thinning progressed in the forest. Thus, gap creation may not increase species diversity at both the gap level and landscape level. However, many studies have found higher species diversity in gaps than in closed forest, as expected under the gap partitioning hypothesis (Ricklefs, 1977; Busing and White, 1997; Schumann et al., 2003; Kumar and Ram, 2005). Under this hypothesis, species exhibit niche differentiation along a gap-size gradient. In contrast, Whitmore and Brown (1996) found no fundamental niche differentiation between canopy gaps of different sizes in a natural rain forest, suggesting that gap-creation may have no significant effect on diversity in some forests. Controversy over the relationship between gap-creation and biodiversity revolves around whether or not the species composition and structure in new gaps will approach that of older, existing gaps as the new gaps fill in (i.e. as the canopy closes). If new gaps come to resemble old gaps then artificial gap creation may not enhance tree species diversity. Otherwise, species diversity could be increased by gap creation. In natural forests, biodiversity likely increases shortly after gap creation and decreases with canopy closing, because gaps will come to resemble the natural forest (in species composition) over time, owing to plant succession. For planted forests, however, the composition and structure in gaps may be quite distinct from the rest of the forest, even after canopy closing. A characteristic of planted forest ecosystems is their consistently low species diversity (Coates and Burton, 1997). Gaps in planted forest ecosystems may provide habitat for native species to germinate, survive and grow. When native tree species become canopy dominants in gaps, the species diversity of both the canopy and its understory has been shown to increase significantly in comparison with the original (pre-disturbance) forest, potentially leading to an overall increase in biodiversity in the planted forest (Dupuy and Chazdon, 2008; Nakamura et al., 2005). Thus, the first hypothesis of this paper is that gap creation in planted forest should enhance diversity of vascular plant.

Studies have found that gap size influences light availability, temperature, moisture, soil water content and nutrient cycling, all variables which may in turn influence gap floristic composition and structure. For example, gaps may lead to changeover in plant life forms due to altered light availability (Naaf and Wulf, 2007; Schumann et al., 2003; Ito et al., 2006). Photophilic species tend to emerge in large gaps, while more shade-tolerant species tend to emerge in smaller gaps. Therefore, different life forms may be found in gaps of different sizes. However, Whitmore and Brown (1996) found there was no fundamental niche differentiation between canopy gaps of different sizes in a natural rain forest. A likely reason why no niche differentiation was observed relates to gap size and the duration of the study. Both a long period of observation and enough large gaps are necessary to observe niche differentiation between gap types. In addition, it can be hard to distinguish if the canopy dominant species in the gaps are highly similar to those species found in the forest itself. In planted forests, however, native species are predicted to emerge in the gaps, leading to a difference in species composition between gaps and undisturbed forest understory. Given enough time and large enough gaps, different life forms may emerge in different gaps. This difference in life forms could lead to higher biodiversity at both the gap level and landscape level in planted forests. Fahey and Puettmann (2008) have suggested that utilizing characteristics of understory plants, for example classifying the understory community into life forms, may further aid in the detection of gap influence. Thus, our second hypothesis is that gaps of different sizes will increase the number of different plant life forms present.

A key concern in how gaps may affect patterns of regeneration is the regeneration of native species (including their germination, growth and survival), especially for climatic climax species.

Whether or not native species can successfully regenerate in gaps is an important precondition for the near-natural cultivation of planted forest. Some tree species have been shown to display a preference for particular gap sizes, in that they require a certain amount of light or a minimum gap size in order to regenerate (Whitmore and Brown, 1996; Myers et al., 2000). For example, Brazil nut saplings were only present in gaps $>95\text{ m}^2$, and were absent in all understorey sites (Myers et al., 2000). If the minimum gap size for a species to regenerate successfully is defined as the ratio of gap diameter to the height of surrounding trees, the ratios range from >2.0 for Scots and Corsican pine, to 1–2 for Sitka spruce and Douglas fir, to 1.0 or less for more shade-tolerant species (Malcolm et al., 2001). Therefore, an important goal for research on the near-natural cultivation of planted forests is to determine whether or not the regeneration of native species, especially that of the climatic climax species, is limited by gap size. It is also important to determine if native species can reach the canopy layer and become dominants. This should be possible given that native species are presumably locally adapted to the climatic and soil conditions of a given gap. Different size gaps will support the regeneration of different species owing to differences in light density and temperature (which vary with gap size). Hence, our third hypothesis is that opening gaps in planted forests will provide the necessary conditions for native species to regenerate, provided that the gaps are of the appropriate size distribution. Establishment of native plant communities in gaps should lead to the development of more natural forest communities as plant succession proceeds.

In the 1960s, the Chinese government organized local farms to build *Pinus tabulaeformis* forests for water and soil conservation on the Loess Plateau, China. In the early 1980s, some of the trees were cut for timber in the forests although logging was banned shortly thereafter. However, some gaps had all ready been created in the logged planted forests. Since 1986, several of these pine forests have been monitored for the purpose of ecological and hydrological research by the Yichuan Field Station of Soil and Water Institute, Chinese Academy of Sciences. Research has revealed a significant difference in plant species composition and structure between the undisturbed forest understory and the new gaps, especially in the emergence of native species such as the climax species, *Quercus liaotungensis*. We made use of this watershed in order to test the three hypotheses listed above. The goals of our study were to estimate the influence of gap creation on planted forest regeneration and to evaluate the potential of this approach for near-natural cultivation strategies.

2. Materials and methods

2.1. Study site

This research was carried out in the Nanchuan watershed, Shaanxi Province, China ($110^{\circ}01'–110^{\circ}07'$ E, $35^{\circ}17'–35^{\circ}25'$ W). The watershed has a mainland monsoon type climate with an average annual precipitation of about 584.4 mm and a mean annual temperature of 9.7 °C. Altitude in the watershed ranges from 800 m to 1450 m. The soil is gray forest soil. The clay, silt and sand contents are 36.80%, 24.33%, and 38.87%, respectively (USA soil taxonomy). The organic matter content is $13.6 \pm 1.28\text{ g kg}^{-1}$ (mean \pm SD); soil total N content is $1.54 \pm 0.24\text{ g kg}^{-1}$; and soil total P content is $1.42 \pm 0.38\text{ g kg}^{-1}$. The natural vegetation is typical deciduous broad-leaf forest of a warm temperate zone, and the climatic climax community is mixed forest with both broad- and needle-leaf species. The dominant canopy species include *Quercus liaotungensis*, *Pinus tabulaeformis* and *Betula platyphylla*. However, both the original and secondary forests at this site were destroyed

prior to the 1960s, leading to serious soil and water losses in this region.

2.2. Experimental design

Eight *Pinus tabuliformis* forests in Nanchuan watershed, planted between 1963 and 1964 with 1667 stem/hm² as the original stand density, were selected for use in this study. The mean forest area was 16.8 ± 4.9 ha (mean ± S.E), with a range of 9.6 to 28.5 ha. Gaps in the forest were created in 1985 and closed about 14–18 years after their creation. In 2007, we selected canopy gaps (in each of the 8 stands) with areas ranging from 4 m² to 4508 m². Mean canopy tree height was 12.6 ± 1.4 m (mean ± S.E). In order to compare plant composition in the gaps and the forest, control plots with similar topographical and orographical characteristics to the gaps were established at least 15 m from the border of each gap edge. The distance between any two gap plots was at least 40 m (edge to edge). Those distances are greater than the canopy tree height, and presumed to be sufficient to avoid any influence from an open canopy. From July to October, a total of 722 canopy gap plots and 722 forest plots were selected. Next, the plots were categorized according to habitat type: forest (722 plots), small gaps (5–25 m², 586 gap plots), medium gaps (26–150 m², 130 gap plots) and large gaps (151–450 m², 6 gap plots).

Quadrats used to sample herbaceous communities were 1 m², with 2–3 replicates per plot, while quadrats used to sample shrub and tree communities were 5 m² with nested sampling. The number of quadrats placed in a plot was roughly proportional to plot size. Data collected in each quadrat included plant species, height, basal diameter (for trees and shrubs), diameter at breast height (DBH), and abundance; general information about the gap area, gap shape, slope gradient, and slope aspect was also collected for each quadrat.

From each quadrat, three soil samples for nutrient content analysis were collected from each 10 cm layer between 0 and 50 cm depth using a stainless steel auger in October, 2007. These soil samples underwent standard analysis for nutrient contents (Lu, 2000). The available N was determined by the continuous alkali-hydrolyzed reduction diffusing method. Available P was measured by the Olsen method.

2.3. Data analysis

For quantification purposes, we defined gaps as the vertical projection of a given opening in the forest canopy. Gap size was calculated using a method (Lima, 2005) that divides the gap into triangles, calculates each triangle's area, and then sums all triangles to obtain total gap area.

The individual gap plots and understory control plots were considered experimental units in this design. To calculate the species-area curves (SACs) of the four habitat types (small gaps, medium gaps, large gaps and understory), we selected 40 small gap plots, 40 medium gap plots, 6 large gap plots and the 86 paired control plots (understory) at random. For each plot, we calculated the mean number of species in all quadrats and the total number of species found in each plot, for SAC construction (Shmida, 1984). SACs were constructed using the mean value of all plots belonging to a given habitat type.

To compare vascular plant diversity among the four habitat types, Shannon indices (Shannon and Weaver, 1949) (log base 2) and evenness indices (Pielou, 1969) were calculated for each gap and understory plot. Diversity indices were compared between gaps and their control plots using a random pair *t*-test, while the differences among small gaps, medium gaps and large gaps were determined using one-way ANOVAs.

To compare plant density among the four habitat types, we first calculated the individual densities of herbs, shrubs and trees in each plot. Next, the herb densities were each calculated for an area of 1 m², for easier comparison with the results of other studies; shrub and tree densities were standardized to an area of 100 m². Density was compared between gaps and their control plots using a random pair *t*-test, and among small, medium and large gaps using one-way ANOVAs.

An importance value (IV) for each species was calculated in each gap and understory plot. In each plot, the IV for each tree species was calculated as: [(relative density + relative dominance + relative frequency)/3] × 100%; the IV for each shrub species was calculated as: [(relative density + relative frequency + relative coverage)/3] × 100%; and the IV for each herb species was calculated as: [(relative height + relative aboveground biomass)/2] × 100%. The mean IV for each species was calculated in each habitat type.

To understand the regeneration of *Q. liaotungensis*, *P. tabulaeformis*, and *P. davidiana*, the tree species with the highest IVs (Table 1), we counted the number of individuals (per plot) in each basal diameter class (classes were composed of 2 cm intervals). The mean number of individuals in each basal diameter class was calculated for each habitat type.

The similarity in species composition between any two kinds of habitat types (i.e. forest understory, small, medium or large gaps) was calculated as: Index of similarity (IS) = 2C/(A + B) × 100, where C is the number of common species (found in both the plot types), and A and B are the total number of species in plot type A and in plot type B, respectively.

To investigate possible relationships between species composition and habitat parameters, a direct ordination method was used, the Canonical Correspondence Analysis (CCA). This analysis both describes variation in species composition and environment among sites and, at the same time, evaluates which environmental factor explains the most variation in the species composition (ter Braak, 1986). To perform the analysis, species density was used for the main matrix and the environmental (or secondary) matrix contained the following variables: gaps area, slope aspect (south, north, west and east), slope gradient, topographic position (ridge, slope and valley), altitude, available N, and available P. Selection of these variables was based on a preliminary Principal Component Analysis (PCA) applied to all gap parameters (measured variables). Parameters with high eigenvector values in the first and second axis of the PCA were chosen for inclusion in the CCA. When parameters were strongly colinear, only one was used in the analysis. Interpretation of the ordination diagrams obtained (biplots) from the CCA followed ter Braak (1986).

In both ordination analyzes, proportion data were arcsine square root-transformed while other data were log-transformed (Digby and Kempton, 1987) in order to obtain normality. All multivariate analyzes were implemented using the CANOCO package, and eigenvalues were assessed for significance with Monte Carlo permutation tests. The statistical methods were implemented using the SPSS statistical package.

3. Results

3.1. Effect of gap size on species composition and structure

3.1.1. Species-area curves and vascular plant diversity index

A total of 112 plant species were found in total, out of which 21 were trees, 29 shrubs and 62 herbs. There were 101 species found in gaps, 94 species found in the forest understory and 83 species found in both the understory and in gaps.

The SACs of tree, shrub and herb communities revealed that the number of species initially increased with area, but then gradually

Table 1
Plant individual density (individual/100 m² for trees and shrubs, individual/m² for herbs) and important value (IV) in gaps and understory.

Species	Understory		Small gaps		Medium gaps		Large gaps	
	Density	IV	Density	IV	Density	IV	Density	IV
<i>Trees</i>								
<i>Q. liaotungensis</i>	70.25	52.08	226.95	47.94	415.80	66.26	276.00	16.59
<i>P. tabulaeformis</i>	36.93	27.82	91.80	17.49	156.16	24.57	421.71	24.62
<i>P. davidiana</i>					14.03	2.25	870.25	51.62
<i>U. pumila</i>			53.55	12.83			2.80	0.17
Others	28.05	20.83	102.9	21.74	37.4	6.92	104.5	7.00
<i>Shrubs</i>								
<i>R. hugonis</i>	12.39	20.86	51.92	26.96	32.5	17.32	22.18	25.13
<i>O. davidiana</i>	8.27	14.63	34.22	18.54	13.5	7.26	10.37	11.06
<i>F. suspensa</i>	11.52	20.24	31.17	16.18	7	4.02	0.60	0.63
<i>S. salicifolia</i>	10.16	18.66	7.08	3.72	27.5	14.69	8.54	9.12
<i>C. korshinskii</i>	3.57	6.61	8.26	4.56	0.5	0.35	9.56	11.56
<i>L. bicolor</i>	0.27	0.52			11	5.93	10.37	2.25
<i>R. corchorifolius</i>	5.43	9.58	14.16	5.51	47.5	25.46	1.83	2.05
<i>L. japonica</i>	1.04	1.79	22.42	11.60	14.5	7.70	7.33	8.11
Other	4.42	7.11	17.70	12.93	30.26	17.27	17.69	30.09
<i>Herbs</i>								
<i>C. lanceolata</i>	55.21	44.93	48.52	37.06	35.64	19.84	43.51	33.13
<i>P. heterophylla</i>	0.54	0.51	6.51	5.01	18.22	10.14	8.17	6.25
<i>A. argyi</i>	6.83	5.68	14.55	10.94	6.37	3.55		
<i>S. sibiricus</i>	3.59	2.90	2.25	1.78	12.45	6.93	13.31	10.07
<i>L. leontopodioides</i>	5.27	4.21	0.78	0.62	19.54	10.88		
<i>P. tanacetifolia</i>					5.94	3.31	14.53	10.87
<i>H. lyrata</i>	6.49	5.34	3.92	2.89	16.28	10.04	4.49	3.46
<i>R. cordifolia</i>	5.23	4.37	13.23	10.03	5.25	2.82	5.01	3.87
<i>C. indicum</i>	6.47	5.38	2.56	2.11	9.30	5.24	15.15	11.99
Others	32.98	26.68	39.21	29.56	51.62	27.25	28.48	20.36

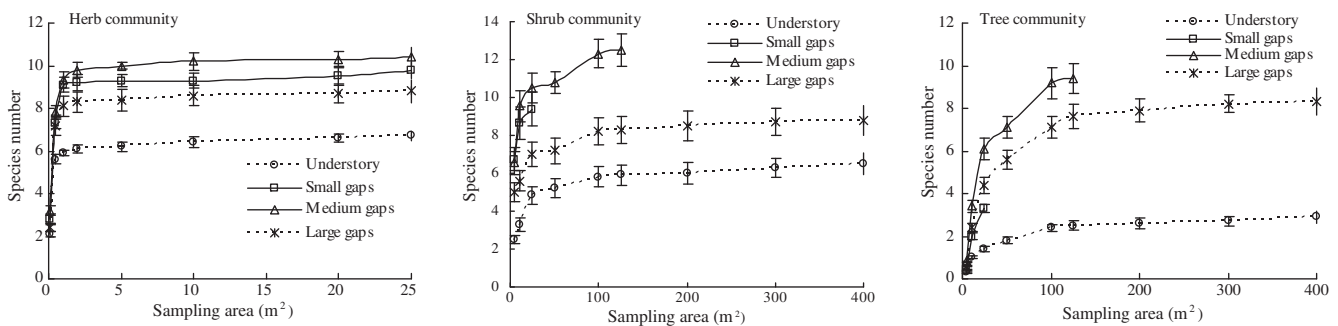


Fig. 1. Species–area curves of herb, shrub, and tree communities at understory and gaps.

reached a plateau (Fig. 1). The SACs for gaps of all sizes were significantly higher than those for the forest understory, suggesting that the species richness in gaps was higher than that in the forest understory. In addition, species richness was greatest in medium gaps for trees (9.24 ± 0.67 species/100 m²), shrubs (12.32 ± 0.83 species/100 m²) and herbs (9.35 ± 0.37 species/m²). Compared to large gaps, small gaps had many more shrub and herb species, but fewer tree species.

Shannon indices were also maximized in medium gaps for trees (2.56 ± 0.17), shrubs (1.96 ± 0.11) and herbs (1.28 ± 0.12), and diversity was also significantly greater in gaps of all sizes than in control (forest) plots (Fig. 2).

Herbaceous species evenness was highest in medium and large gaps (Fig. 3). Evenness was greatest in large gaps for shrubs, and in small gaps for trees. There were no significant differences in tree species evenness among the understory, medium gaps and large gaps.

3.1.2. Plant density and importance value (IV)

Analysis of species abundance data (as density or coverage) revealed that only a few forest understory and gap species could

be considered dominants (Table 1). Out of a total of 112 species, 4 trees (*Q. liaotungensis*, *P. tabulaeformis*, *P. davidiana* and *Ulmus pumila*), 8 shrubs (*Rosa hugonis*, *Ostryopsis davidiana*, *Rubus corchorifolius*, *Forsythia suspensa*, *Lonicera japonica*, *C. Korshinskii*, *Spiraea salicifolia* and *Leapedeza bicolor*) and 9 herbs (*Carex lanceolata*, *Patrinia heterophylla*, *Artemisia argyi*, *Spodiopogon sibiricus*, *Leontopodium leontopodioides*, *Potentilla tanacetifolia*, *Hemistepta lyrata*, *Rubia cordifolia* and *Chrysanthemum indicum*) had an IV $\geq 10\%$, while a large number of species had an IV $< 10\%$ (Table 1). Thus, less than one fifth of the species present were dominants.

Tree density was highest in large gaps and medium gaps, and lowest in the forest understory (Fig. 4 and Table 1). *Q. liaotungensis* is the climax species in this climatic region and was observed in all understory plots and gaps, with maximum density in medium gaps. *P. tabulaeformis*, an important native species for timber production, and soil and water conservation, was also observed in all understory plots and gaps. *P. davidiana*, a pioneer species, was not found in the understory, but was present in small and medium gaps of lower density. In large gaps, a very high density of 870.25 stem/100 m² and an IV of 52.08% indicated that *P. davidiana* was the only dominant species in the pioneer community.

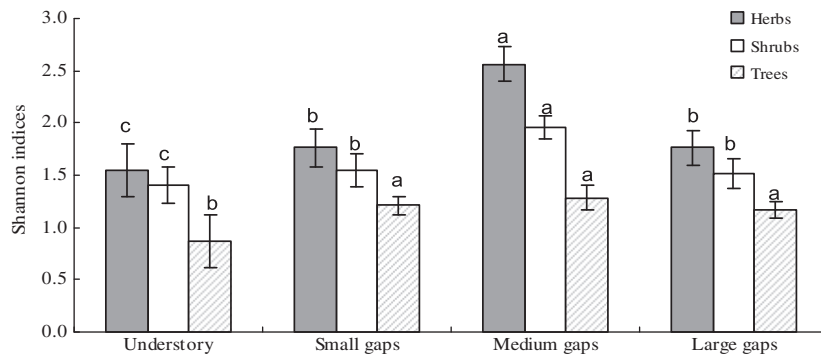


Fig. 2. Comparison of species diversity among understory and gaps.

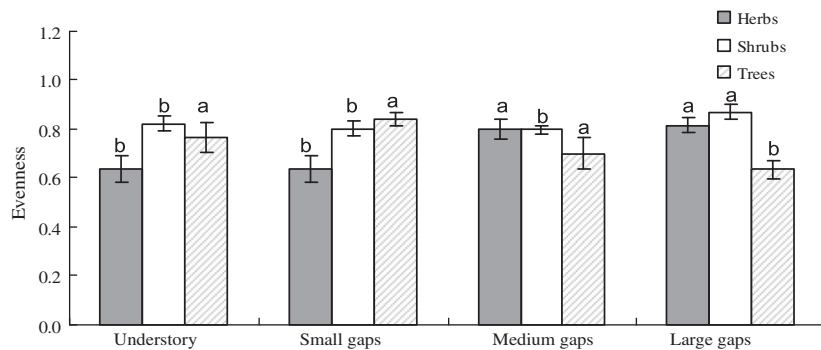


Fig. 3. Comparison of evenness indices among understory and gaps.

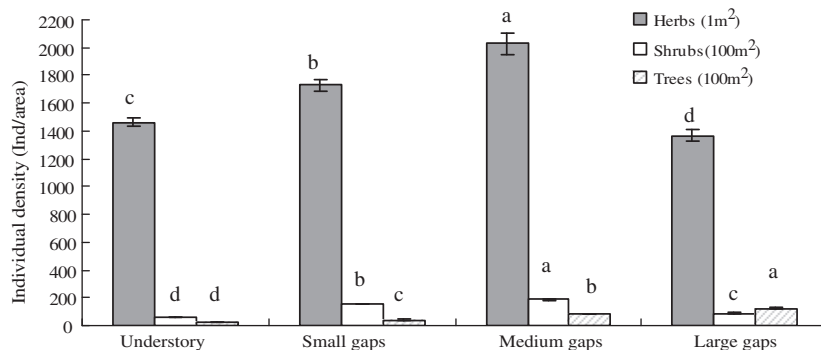


Fig. 4. Comparison of individual density among understory and gaps.

Hence, it appears that medium and large gaps may positively influence the regeneration of trees.

Shrubs achieved the highest densities in small and medium gaps, and the lowest densities in forest understory plots. For the eight shrub species with the highest individual densities (Table 1), maximum density and IV was observed in small gaps for *R. hugonis*, *O. davidiana* and *L. japonica*, in medium gaps for *S. salicifolia*, and in both small and medium gaps for *F. suspensa*, *Caragana Korshinskii* and *R. corchorifolius*. Maximum density and IV was observed in large gaps for *L. bicolor*. In summary, small and medium gaps may support the growth and development of shrubs, some of which could become dominant species in small gaps in early successional stage. Trees only become the dominant species in medium and large gaps.

The density of herbaceous species peaked in medium gaps, while density was lowest in small gaps. The maximum individual densities observed occurred in the understory (*C. lanceolata*), in

small gaps (*A. argyi* and *Rubia cordifolia*), in medium gaps (*P. heterophylla*, *S. sibiricus*, *L. leontopodioides* and *H. lyrata*) and in large gaps (*P. tanacetifolia* and *Chrysanthemum indicum*).

3.2. Similarity of species composition between gaps and forest understory

For the 112 species recorded in our study, 83 species occurred both in gaps and in the understory, indicating that there is a high degree of overlap between these two habitat types (SI = 74.11%).

The SI among understory, small gap, medium gap and large gap habitats in tree species composition ranged from 26.67% (between the understory and large gaps) to 53.85% (between medium gaps and large gaps) (Table 2). The SI among habitat types for shrub species composition ranged from 62.50% (between small gaps and medium gaps) to 76.92% (between understory and small gaps) (Table 3), while that for herbaceous species ranged from

Table 2
Similarity indices of tree among gaps and forest (%).

	Understory	Small gaps	Medium gaps	Large gaps
Understory	100	38.46	30.77	26.67
Small gaps		100	45.45	33.33
Medium gaps			100	53.85
Large gaps				100

Table 3
Similarity indices of shrubs among gaps and understory (%).

	Understory	Small gaps	Medium gaps	Large gaps
Understory	100	76.92	64.29	69.23
Small gaps		100	62.50	71.43
Medium gaps			100	73.33
Large gaps				100

Table 4
Similarity indices of herbs among gaps and understory (%).

	Understory	Small gaps	Medium gaps	Large gaps
Understory	100	55.56	50.00	40.91
Small gaps		100	59.09	55.00
Medium gaps			100	57.69
Large gaps				100

40.91% (between small gaps and large gaps) to 59.09% (between small and medium gaps) (Table 4). In general, the more similar the habitat types, the more similar their species composition. The reason for high similarity among the gaps and understory habitat types was that some species, such as *P. tabulaeformis*, *Q. liaotungensis*, *Rosa hugonis*, *O. davidiana*, *F. suspensa*, *C. lanceolata* and *P. heterophylla*, were present in both gaps of different sizes and in the understory.

3.3. Regeneration of three main tree species

Trees, especially those comprising the canopy, play the most important ecological roles in forest ecosystems. *Q. liaotungensis*, *P. tabulaeformis* and *P. davidiana* were the dominant tree species in our system, as determined by high IV values (Table 1). *Q. liaotungensis* is the climatic climax species in this region, and *P. tabulaeformis* is a very important companion species which can become co-dominant with *Q. liaotungensis* in mixed broadleaf-conifer forests. *P. davidiana* is a pioneer species and a canopy dominant species in the early stages of succession for larger gaps. Thus, these three species are critically important for community succession.

3.3.1. Regeneration of *Q. liaotungensis* and *P. tabulaeformis*

Fig. 5 and Table 5 illustrate the distribution of basal diameter class for *Q. liaotungensis* and *P. tabulaeformis* in forest understory; a power function best describes the distribution. The very low parameter, *a*, in the power function indicates that juveniles of both *Q. liaotungensis* and *P. tabulaeformis* were very small. Indeed, in the understory, most seedlings were less than 1 cm in basal diameter, with the maximum basal diameter recorded being less than 4 cm. Most of the juveniles occurred on sunny slopes. The very low parameter, *b*, in the power function indicates that size-dependent mortality is very high. Parameter *b* can be interpreted as follows: when trees in a given basal diameter class double their basal diameter, the density of the double basal diameter class should decrease to 2^b of the density of the given diameter class. This phenomenon can result from self-thinning caused by horizontal space competition among trees, as described by the 'tile model' (Shimano, 2000).

In small gaps, parameters *a* and *b* of *Q. liaotungensis* and *P. tabulaeformis* were slightly higher in comparison with those of the understory, indicating that the number of juveniles increased and their mortality decreased with increasing gap size (Table 5).

In medium and large gaps, greater values of "a" indicated significantly greater numbers of juveniles, while greater values of "b" revealed a significant decrease in juvenile mortality (Table 5). For example, for *Q. liaotungensis* on south-facing slopes, "a" for

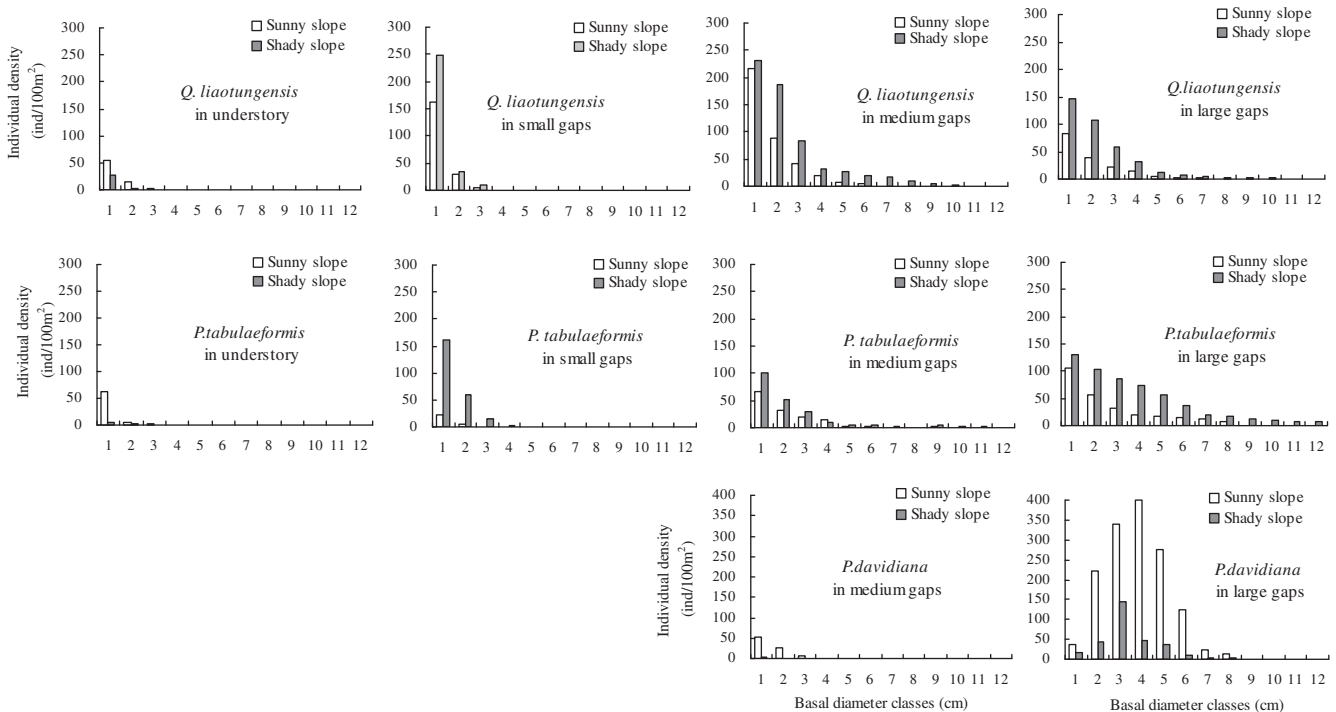


Fig. 5. Changes of plant individual density with the basal diameter.

Table 5
The regeneration power function of *Quercus liaotungensis* and *Pinus tabulaeformis*.

Tree	Slope facing	Understory			Small gaps			Medium gaps			Large gaps		
		a	b	R ²	a	b	R ²	a	b	R ²	a	b	R ²
<i>Q. liaotungensis</i>	South-facing	17.20	-2.254	0.887	39.56	-2.550	0.935	118.04	-1.846	0.838	60.55	-1.897	0.914
	North-facing				56.796	-2.613	0.919	219.67	-1.762	0.786	133.30	-1.834	0.881
<i>P. Tabulaeformis</i>	South-facing	10.62	-1.847	0.962	5.477	-1.869	0.903	47.81	-1.692	0.716	67.215	-0.943	0.966
	North-facing	1.730	-1.876	0.922	62.63	-1.410	0.903	57.486	-1.466	0.853	138.650	-1.015	0.803

$$Y = a \times b.$$

medium gaps was 5.9 times higher than that for the understory, while "b" increased from -2.254 in the understory to -1.846 in medium gaps, indicating that size class density should decrease to 21% and 28%, respectively, when trees in a given basal diameter class double their basal diameter. This phenomenon likely results from self-thinning, i.e. from horizontal space competition among trees. In medium and large gaps, *Q. liaotungensis* and *P. tabulaeformis* became the new dominant species with a sustainable development structure of basal diameter.

For *Q. liaotungensis*, juvenile number was greater in medium gaps than in large gaps, while mortality remained the same. Thus, *Q. liaotungensis* showed enhanced survival and regeneration in medium gaps. *P. tabulaeformis*, however, had enhanced survival and regeneration in large gaps (where juvenile numbers were highest).

The regeneration of *Q. liaotungensis* and *P. tabulaeformis* was influenced by slope aspect. In general, juvenile numbers on shady slopes were greater than those on sunny slopes, and trees with greater basal diameters tended to be found on north-facing slopes.

3.3.2. Regeneration of *P. davidiana*

No seedlings and saplings of *P. davidiana* were observed in the understory and only a few seedlings were found in small gaps. In medium gaps, although there were many seedlings, there were no saplings with basal diameter >4 cm. In the large gaps, the number of seedlings and saplings increased sharply, and the basal diameter distributions were skewed positively (Fig. 5). The highest frequency interval was from 3 to 5 cm. For seedlings with basal diameter less than 4 cm, numbers increased with increasing basal diameters, indicating a decrease in juvenile numbers with time. This phenomenon may be explained by lower germination and survival rates as light availability decreased with canopy closing. Therefore, the pioneer dominant species, *P. davidiana*, may eventually be replaced by *Q. liaotungensis* and *P. tabulaeformis* in large gaps.

3.4. The relationship between species distribution and environment factors

The first two axes in the CCA analysis explained 54.9% of the variance in the relationship between species composition and the environmental variables (Tables 6 and 7). The species-environment correlations and eigenvalues were relatively high, indicating that species abundance variation was well explained by the measured environmental variables. As revealed by the Monte Carlo permutation tests, eigenvalues for the first two axes of all groups were significant, as were the correlations between species composition and environmental variables.

From examination of the canonical coefficients and of correlations between environment variables and the environmental axes showed in Tables 6 and 7, it appears that the first species axis is related to gap area, while the second axis describes slope aspect. This can also be seen in the ordination diagram (Fig. 6).

Gap area can be interpreted as a gradient ranging from low values (at the negative end of axis I) representative of the understory to higher values (at the positive end of the axis) representing large gaps. Most shrubs and trees, such as *Cerasus tomentosa*, had high scores on axis I (Fig. 6), which indicates that they grew preferentially in larger gaps. Herbs, although covering all the gradient space, were more abundant in small and shady environments. Shade intolerant species, such as *Artemisia giraldii* and *Spodiopogon sibiricus*, had high scores on axis II, meaning that they are found in environments with high light availability, with the converse applying to shade tolerant species, such as *Pulsatilla chinensis*.

Table 6
Summary of canonical correspondence analysis (CCA) and Monte Carlo test.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.325**	0.177**	0.158 ns	0.093 ns	
Species–environment correlation	0.924**	0.854**	0.802*	0.710 ns	
Cumulative percentage variance of species–environment relation	35.5	54.9	72.2	82.4	
Sum of all eigenvalues					3.595
Sum of all canonical eigenvalues					0.914

ns = Non significant.

* $P < 0.05$.

** $P < 0.01$.

Table 7
Canonical coefficients and correlations of environment variables with the first two ordination axes (intra-set correlations) and with the samples score (inter-set correlations).

Variable	Canonical coefficient		Intra-set correlations		Inters-set correlations	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Gap area	0.9814	-0.1048	0.920	0.0427	0.9760	0.0500
Slope aspect	0.0935	-1.0256	0.0729	-0.7796	0.0789	-0.9125
Slope gradient	-0.0892	-0.1690	0.0374	-0.1581	0.0404	-0.1850
Altitude	-0.1727	0.6729	0.4464	0.2823	0.4830	0.3305
Slope position	-0.2328	0.4569	-0.3698	-0.3191	-0.4002	-0.3735
Available N	0.0386	0.0428	-0.2254	-0.1027	-0.2439	-0.1202
Available P	-0.1605	-0.2459	-0.2188	0.0295	-0.2368	0.0345

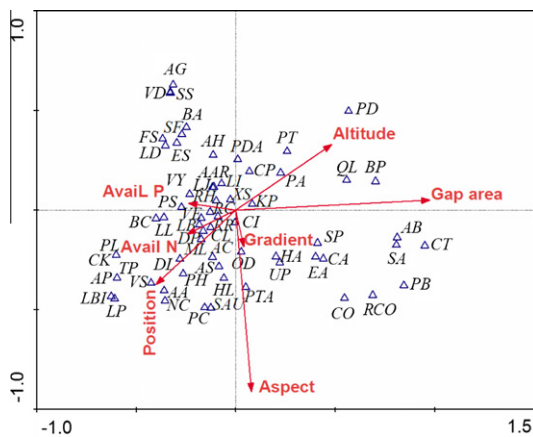


Fig. 6. Ordination diagrams (biplots) obtained from the Canonical Correspondence Analysis (CCA). AA: *Ampelopsis aconitifolia*; AAR: *Artemisia argyi*; AB: *Acer buergerianum*; AC: *Asparagus cochinchinensis*; AG: *Artemisia giraldii*; AH: *Anemone hupehensis*; APA: *rtemisia apiacea*; AS: *Artemisia sacrorum*; BA: *Buddleja alternifolia*; BC: *Bupleurum chinense*; BP: *Betula platyphylla*; CA: *Cotoneaster acutifolius*; CI: *Chrysanthemum indicum*; CK: *Caragana Korshinskii*; CL: *Carex lanceolata*; CO: *Celastrus orbiculatus*; CP: *Crataegus pinnatifida*; CT: *Cerasus tomentosa*; DL: *Dendranthema lavandulifolium*; DP: *Dioscorea polystachya*; EA: *Euonymus alatus*; ES: *Eleutherococcus senticosus*; FS: *Forsythia suspensa*; HA: *Heteropappus altaicus*; HL: *Hemistepta lyrata*; KP: *Koeleruteria paniculata*; LB: *Lepedeza bicolor*; LBI: *Limonium bicolor*; LD: *Lespedeza davurica*; LI: *Lespedeza bicolor*; LJ: *Lonicera japonica*; LL: *Leontopodium leontopodioides*; LP: *Lilium pumilum*; ML: *Medicago lupulina*; NC: *Neottianthe cucullata*; OD: *Ostryopsis davidiana*; PA: *Prunus armeniaca*; PB: *Pyrus betulaeifolia*; PC: *Pulsatilla chinensis*; PD: *Populus davidiana*; PDA: *Prunus davidiana*; PH: *Patrinia heterophylla*; PL: *Polygala tenuifolia*; PS: *Polygonatum sibiricum*; PT: *Pinus tabulaeformis*; PTA: *Potentilla tanacetifolia*; QL: *Quercus liaotungensis*; RC: *Rubia cordifolia*; RCO: *Rubus corchorifolius*; RH: *Rosa hugonis*; RR: *Raphanus raphanistrum*; SA: *Spiraea salicifolia*; SAU: *Scorzonera austriaca*; SF: *Sophora flavescens*; SP: *Syringa pекinensis*; SS: *Spodiopogon sibiricus*; TP: *Thalictrum petaloideum*; UP: *Ulmus pumila*; VD: *Viola dactyloides*; VE: *Vicia sepium*; VS: *Viburnum schensianum*; VY: *Viola yedoensis*; XS: *Xanthoceras sorbifolia*.

From the lower left-hand corner to the upper right-hand corner of the ordination plot, species could be divided into three life forms: herbs, shrubs and trees. Examination of the plot then reveals the effects of gap area and slope aspect on each life form.

4. Discussion

4.1. Effect of gap size on the vascular plant diversity of planted forest

A significant difference in plant species composition between forest gaps and understory was found after more than 20 years of plant succession. The species richness and Shannon indices of all gap sizes were significantly higher than those of the understory. Hence, our first hypothesis, that creating gaps in planted forest can increase vascular plant diversity, was supported.

A total of 112 plant species were found in all forest and gap plots, out of which 11 plant species, most shade tolerant species, were only present in the understory. There were 18 species only found in gaps, most of which were shade intolerant species. Some studies (Selmants and Knight, 2003; Romell et al., 2008) have found that gap creation can improve light availability to the forest floor, which can increase the establishment and growth of shade intolerant species. However, on the other hand, the creation of gaps may negatively influence the establishment and propagation of shade tolerant species (Schumann et al., 2003; Nichols et al., 1998). The germination, survival and growth of shade-tolerant and shade-intolerant tree species has frequently been correlated with gap size (Coates and Burton, 1997; Arevalo and Fernandez-Palacios, 2007). In general, both the species richness and the biodiversity of gaps were higher than in the forest understory (Naaf and Wulf, 2007). Furthermore, the Shannon indices of trees, shrubs and herbs were highest in medium gaps. This result is consistent with the intermediate disturbance hypothesis which postulates that maximum diversity is achieved under conditions of intermediate disturbance size, frequency or intensity (Connell, 1978; Roberts and Gilliam, 1995). In this study, the high plant species richness and diversity in medium gaps was driven by herbs, shrubs and trees (Fig. 1), but especially by the herbs. In medium gaps we expect high species diversity, in comparison with small gaps, because the gaps can support the establishment of more shade-intolerant species before canopy closure, and the rest of the stand can support shade-tolerant species (Decocq et al., 2004; Torras and Saura, 2008). However, if the gaps exceed a critical size, a few light-demanding, competitive species will dominate in the earliest stages of succession (Decocq et al., 2004) resulting in low species

diversity. Therefore, medium gaps tend to have the highest plant diversity.

In contrast to this pattern, other studies (Hubbell et al., 1999; Whitmore and Brown, 1996) have found that new gap creation does not increase tree species diversity in tropical forests. The increase in species diversity after gap creation is temporary and disappears as gaps thin out. Hence, gaps won't increase species diversity at both the level of the gap and the landscape after the canopy closure. In our research, the canopy over the gap closed about 14–18 year after the gap was created. The species diversity of trees, shrubs and herbs in gaps was higher than in the understory, from the completion of canopy closing to the present day. Gap and understory plots also differed in plant species composition and structure. Canopy species in the medium and large gaps were largely natives, including *Q. liaotungensis*, *P. tabulaeformis*, *P. davidiana*, and *Ulmus pumila*, while *P. tabulaeformis* formed the canopy exclusively in the understory. Based on the basal diameter distribution of the 3 most common tree species (*Q. liaotungensis*, *P. tabulaeformis* and *P. davidiana*.) in the medium and large gaps, these patches should develop into mixed broadleaf-conifer forest, instead of mono-dominant pine forest. Thus far in our study, there is no evidence of decreasing vascular plants diversity in gaps with plant succession.

4.2. Effect of gap area on regeneration

Gap size influenced individual species emergence rates in the gap. For example, only 11 species emerged as seedlings in the understory, *Koeleruteria paniculata* emerged only in large gaps, and *Rhus typhina* only emerged in the medium gaps. In addition, although some species did emerge in different sized gaps, they frequently did so at significantly different densities. For example, the density of *P. davidiana* in large gaps was 62 times greater than in the medium gaps; the density of *R. corchorifolius* was 26 times greater in medium vs. large gaps; and, the density of *C. indicum* was 5.9 times greater in large vs. small gaps. Other studies have also found that some species only regenerate in certain sized gaps. For example, in a retrospective analysis of old logging gaps, the density of naturally regenerating western hemlock was positively correlated with gap size (Coates and Burton, 1997). Likewise, paper birch was found only in gaps >2400 m² while Brazil nut saplings were only present in gaps >95 m² (Myers et al., 2000).

In addition, gap size influenced the pattern of regeneration. As indicated by the power function of the basal diameter distribution, *Q. liaotungensis* and *P. tabulaeformis* juveniles occurred infrequently in small gaps but reached very high densities in both medium and large gaps. Furthermore, juvenile mortality also varied with gap size.

4.3. Effect of gap area on plant life form

The CCA analysis revealed that the distribution of plant life forms was influenced significantly by gap size 30 years after the creation of the gaps. For example, the dominant species in small gaps tended to be shrubs (which may be replaced by trees as succession proceeds), while trees dominated in medium and large gaps. Although some tree species could germinate and survive in small gaps, no seedlings were ever observed to grow into saplings. We found that different sized gaps had different dominant life forms, as shown by other studies (Schumann et al., 2003; Selmanns and Knight, 2003). Moore and Vankat (1986) found that shrubs, ferns and herbs exhibited sensitivity to a variety of forest gap types. Many grass and sedge species were found exclusively in harvest gaps (Schumann et al., 2003). Many of the species found only in the gaps were typical light-demanding plant species. Hence, in support of our second

hypothesis, our results indicate that different species belonging to similar life forms may tend to occur in similar gaps.

Gap size influenced the distribution of plant life forms, via its effects on light availability (Schumann et al. 2003, Ito et al., 2006). One study (Ito et al., 2006) examining the relationship between gap size and light availability found that seedling density increased significantly with increasing gap size, because the micro-environment in large gaps was brighter and warmer than in smaller gaps, increasing the favorability of conditions for germination and establishment by some species. Variation in light availability in different sized gaps may lead to the differential response of plant life forms, as different species vary in their growth requirements. In addition, gap size may also influence temperature, moisture and the cycling of nutrients and water in the forest, which also can influence the plant life form distribution.

4.4. The role of gap size in promoting near-natural cultivation for planted forests

Recently, the use of near natural management practices with planted forests has become an important concept in ecosystem management. A key question concerning this management strategy is whether or not native species, especially the local climax species, can colonize planted forests and grow to become canopy dominants (Taki et al., 2010). In this study, we found that the climatic climax species, *Q. liaotungensis*, and other native species, including *P. tabulaeformis* and *Ulmus pumila*, could colonize and grow into canopy dominants in medium and large canopy gaps. The pioneer species, *P. davidiana*, could become the canopy dominant only early on in succession in the larger gaps. Some native shrub species, such as *Rosa hugonis*, *Ostryopsis davidiana*, *Forsythia suspense* and *Spiraea salicifolia*, regenerated in gaps of all sizes, and also came to dominate in small gaps in early successional stages. In summary, creating gaps in planted forest facilitated native species colonization and regeneration, and led to the dominance of some native species in specific sizes of gaps.

Another key question for near natural cultivation is whether or not the dominant gap species exhibits the appropriate age or basal diameter structure to promote its further successful regeneration. In this study, *Q. liaotungensis* and *P. tabulaeformis* (two canopy dominants) showed the requisite basal diameter structure in both medium and large gaps. For example, *Q. liaotungensis* and *P. tabulaeformis* both had pyramid-shaped basal diameter structures, indicating their likely future sustainable development in medium and large gaps.

A final key question for near natural cultivation is whether planted forests may meet objectives for species diversity conservation and sustainable forest management (Hunter, 1990; Burton et al., 1992; Moore and Allen, 1999). In our study, gaps of different sizes supported the colonization and development of different life forms. For example, small gaps promoted shrubs as canopy dominant species in an early successional stage (about 30 years after gap creation), while medium and large gaps promoted trees likely leading to the eventual development of mixed broadleaf-conifer forest. On sunny slopes, the communities in large gaps resembled mixed broadleaf-conifer forest where *Q. liaotungensis* was dominant, and broadleaf-conifer forest where *P. tabulaeformis* was dominant. Therefore, the creation of gaps of different sizes may provide a chance to conserve different assemblages of species, in support of our third hypothesis.

Gap size and frequency could be easily manipulated during silvicultural interventions, and, hence, the creation of forest gaps may be of practical value for guiding forest management plans (Myers et al., 2000). Further elucidation of the relationships among regeneration characteristics, microclimate and gap size or shape, could allow for the adaptation of management approaches to encourage

the regeneration of species of particular concern (Myers et al., 2000). This study showed that creating gaps greater than 26 m² may favor the growth and dominance of native tree and shrub species. If 26 to 150 m² gaps were created, climax species, such as *Q. liaotungensis* and *P. tabulaeformis* in our study, may quickly dominate the canopy, potentially reducing the time for plant succession. If 150 m² or larger gaps were created, the climax species may take a very long time to become dominant because early successional pioneer species would be so well established. Studies of forest gap dynamics have shown that gap-based management approaches could be successful for forest regeneration (Coates and Burton, 1997; Romell et al., 2008).

Gap creation is, without a doubt, one of the most important regeneration techniques available for use in planted forests. However, other regeneration techniques, such as weed control and sowing native seeds, are also important and could influence the results of gap creation. Hence, an integrated approach that considers interactions among techniques should be considered in the management of planted forest. For example, forest managers have found that weed species can compete strongly with seedlings and saplings for resources such as light, nutrients and water (Romagosa and Robison, 2003; Ramsey et al., 2003; Benayas et al., 2005). Therefore, the germination, survival, and growth rate of seedlings and saplings are strongly influenced by both weeds and gaps. Especially in small gaps and in the forest understory, competition for light may result in a high mortality rate for tree seedlings. This competition by weeds for light and other limiting soil resources would therefore likely reduce tree colonization success and subsequent growth rates, especially of pioneer species in medium and large gaps. Hence, weed control may accelerate the development of young stands, leading to increased survival and growth rates of native trees (Romagosa and Robison, 2003; Benayas et al., 2005). In addition, gap regeneration can also be strongly influenced by seed availability (Howlett and Davidson, 2003), suggesting that artificial disturbances, such as sowing seeds (Guariguata and Pinard, 1998; Howlett and Davidson, 2003) or changing the behavior of seed dispersers in gaps (Joseph and Wunderle, 1997), could influence future tree species composition and structure in both forest gaps and understory. Therefore, other regeneration techniques should be considered when using gap creation to facilitate the transformation of planted forest to a more natural state.

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