Vegetation Trajectories of Korean Red Pine (*Pinus densiflora* Sieb. et Zucc.) Forests at Mt. Seorak, Korea

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The vegetation dynamics of Korean red pine (*Pinus densiflora*) forests were investigated at Mt. Seorak, Korea. Our Detrended Correspondence Analysis (DCA) classified the forests into four types: ridge top, upper slope, lower slope/ hill, and streamside. The ridge top forests were likely to sustain themselves, as suggested by the large proportion of seedlings and saplings (89% at <25 years old) and the relatively high density of *P. densiflora* (2388 stems ha⁻¹). Periodic disturbances, such as flash floods, made the streamside inhospitable to late-successional species. Such conditions may have provided a favorable environment for the recruitment of *P. densiflora* seedlings through increased solar radiation and decreased competition with other species. On the upper slopes, the dominance of *Quercus* seedlings and saplings (63% at >25 years old, and a density of 3263 stems ha⁻¹) suggests a transition from pine to oak forest. Extensive human interventions appeared to arrest the natural succession from pine to oak forests on the lower slope/hill, while encouraging invasions by forest-edge and introduced species (e.g., *Rosa multiflora* and *Robinia pseudoacacia*).

Keywords: dynamics, forest, landscape, oak, pine

Pinus densiflora (Korean red pine) occurs in the subtropical, temperate, and sub-boreal climate zones of Asia, mostly in eastern China, the Korean Peninsula, and the Japanese Archipelago (Chung and Lee, 1965; Mirov, 1967; Richardson, 1997). Its latitudinal range on the Korean Peninsula is from Mt. Halla, on Jeju Island in South Korea (N 33° 20'), to Jeungsan, in North Korea (43° 20') (Chung and Lee, 1965). The most favorable soil type for this species is welldrained sand or gravel that is weathered from granite and eroded by storm waters during the monsoon months in summer (Lee, 1995). With such a wide range of tolerance, P. densiflora normally occurs on the thin and infertile soils of rock outcroppings, weathered rocks, ridge tops, and the sandy or pebble shores of streams. It also can grow well in disturbed soils along both mountain slopes and bases after forest thinning or brush removal near human settlements (Lee, 1976; Toyohara, 1981, 1984; Lee and Hong, 2001; Lee, 2002).

These *P. densiflora* forests are valued by Korean people for numerous amenities to basic life (e.g., material for buildings and ships, fuel, and oils such as terpenes), as well as for aesthetics, recreation, and biological diversity (Lee et al., 1983; Son and Hwang,

1990; Youn and Kim, 1992; KFRI, 1999). Therefore, the expansion of these forests, through artificial plantings and maintenance, has been encouraged by Korean governments since early in the 20th Century (Chun, 1993). However, natural stands of *P. densi-flora* have declined to only about one-third of their extent in the early 1900s for several reasons, including over-exploitation under Japanese occupation (1910-1945), the Korean War (1950-1953), pest defoliation, wildfire, and negligence. Such losses are a concern among forest managers in Korea because of the reduction in forest products and biological diversity (KFS, 2002).

The classifications, species compositions, and physiognomy of *P. densiflora* forests at Mt. Seorak in eastern Korea have been widely investigated (e.g., Park and Hong, 1959; Baek and Yim, 1983; Lim et al., 1983; Yim and Baik, 1985). Recently, Lee et al. (1984) have classified seven types of Korean red pine forests in that region, while Chun (2001) and Hong (2004) have characterized six types there. However, most of these reports have focused on phytosociological descriptions; very little has been studied concerning the dynamics and processes of *P. densiflora* vegetation in relation to abiotic factors. Therefore, the purposes of our study at Mt. Seorak were to (1) characterize the major types of *P. densiflora* forests, (2) investigate the soil-vegetation relationships among these

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types, and (3) project succession trajectories for Korean red pine vegetation. We also hoped that our results could provide information and guidance in the conservation and management of *P. densiflora* forests.

MATERIALS AND METHODS

Study Area

Mt. Seorak (1708 m above sea level) is located on the east-central Korean Peninsula (Fig. 1). Pulguksa granite, formed in the Cretaceous Period, is the major bedrock beneath thin and infertile coarse sands (Lee, 1999; NPAK, 1999). From 1971 to 2000, its mean annual temperature and precipitation were 12°C and 134 cm, respectively (KMA, 2001). This region was the southern limit for migration of northern species during the Tertiary Period, followed by the migration of southern species in the Quaternary Period (Yim and Baik, 1985). Despite more recent exploitation and destruction by humans, these forests have been relatively well-preserved. Because of its significance as representative vegetation in this region, Mt. Seorak was designated as a biosphere reserve by UNESCO in 1982. Its vegetation is best described as temperate deciduous forests dominated by oaks (Quercus spp.), but mixed with coniferous trees at lower and higher elevations. P. densiflora forests constitute approximately 11% of all species, in 21 different vegetation types, at Mt. Seorak (Yim and Baik, 1985; Hong, 2004). Yim and Baik (1985) have found naturally occurring *P. densiflora* forests in rock outcroppings, ridge tops, and slopes, as well as in disturbed deciduous forests and pebble shores of streams in that area.

Vegetation Sampling and Analyses

Vegetation was sampled from May to September in 2000, 2001, and 2002. In all, 127 plots were established at four landscape positions: ridge top (n = 25), upper slope (n = 22; elevation \geq 150 m above sea level), lower slope/hill (n = 37; <150 m), and streamside (n = 43). Plot sizes were based on stand heights, and varied from 5×5 m (understory trees < 5 m tall) to 25×25 m (overstory, >8 m). All plants in each plot were identified by species, following Lee (1996). The frequency and dominance (Braun-Blanquet, 1964) in each plot were also determined for all herbaceous plants, woody seedlings, shrubs (0.8 to 2 m), understory trees (2 to 8 m), and overstory trees, as were the densities of all woody plants and the basal areas of the understory and overstory species. Ages of the P. densiflora stems (>2 cm diameter at breast height; DBH) were estimated with a linear regression model (Samuels and Witmer, 2003). This model was based on tree ring counts and DBH for each landscape position (ridge top: n = 36, r = 0.58, p = 0.0002; upper



Figure 1. Geographic location of the study site at Mt. Seorak, Korea.

slope: n = 33, r = 0.56, p = 0.0007; lower slope/hill: n = 38, r = 0.65, p < 0.0001; and streamside: n =95, r = 0.70, p < 0.0001). These stems were then classified into three age groups (<25 years, 26 to 50 years, and >51 years old) for each position. All stems of <2 cm DBH were assigned to the youngest group. Shrub and understory tree species were also listed for each position. The dominance values for 28 herbaceous (>30% frequency) and 14 woody (>20% frequency) species were converted to the Maarel (1979) scale (1 to 10), and subjected to Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980; McCune and Mefford, 1999) for ordination. These plots were also classified by DCA, based on six landscape characteristics: elevation above sea level, species richness, and total coverages of herbaceous, shrub, understory, and overstory vegetation. Those characteristics were compared by one-way analysis of variance (ANOVA), followed by Newman-Kuel's pairwise mean comparison at the 95% confidence level (Samuels and Witmer, 2003).

Soil Sampling and Analyses

Soil samples were collected from 40 randomly selected plots at the four landscape positions (ridge top, 9; upper slope, 12; lower slope/hill, 8; and streamside, 11). In each plot, four samples were collected from the A₁-horizon (top 20 to 25 cm), then pooled and air-dried. The distribution of soil particle sizes (i.e., gravel, >2 mm in diameter; sand, 0.05 to 2 mm; silt and clay, <0.05 mm) was determined by successive sieving through 2-mm and 0.05-mm mesh screens. Moisture retention capacity was calculated by subtracting the samples' dry weights (48 h at 105°C) from their saturation (with H₂O) weights. Chemical analysis was conducted for samples that passed through the 2-mm sieve. Electrical conductivity (EC) and pH were measured in a 1:5 mixture of

soil and distilled water with a conductivity meter (Conductmeter Model CA-2A; TOA Electric, USA) and a glass electrode (Accumet Model 50; Fisher Scientific, USA), respectively. Cation exchange capacity (CEC) was determined by the ammonium acetate method, while concentrations of organic matter, total nitrogen, and reactive phosphorus were measured according to the Tyürin, Kjeldahl, and Lancaster methods, respectively. Calcium and magnesium were determined by EDTA titration, and potassium was measured colorimetrically (RDA, 1988). These soil parameters were compared by one-way analysis of variance for differences among landscape positions, followed by Newman-Kuel's procedure at the 95% confidence level (Samuels and Witmer, 2003).

RESULTS

Physiognomy of Korean Red Pine Forests

Six landscape characteristics for the P. densiflora forests were determined at the four landscape positions (Table 1), and the general physiognomy was described for different locations (Fig. 2). Elevation did not differ significantly between the ridge top and the upper slope, nor between the lower slope/hill and streamside, but it did between those two pairings. Herbaceous cover was not statistically different between the upper slope and the lower slope/hill, but was higher than for the ridge top and the streamside positions. The latter pairing did not differ significantly in their herbaceous covers. However, the lower slope/hill and streamside had less understory cover than did the other two positions, although those differences were not statistically significant. Shrub cover and species richness were lowest on the ridge top; differences among the other positions were not statistically significant. Likewise, the ridge top had the lowest overstory

Table 1. Pysiognomy of *P. densiflora* forests in four landscape positions at Mt. Seorak, Korea. Each characteristic is expressed as a mean \pm SE. Values followed by the same letter within a column are not statistically different at p = 0.05, based on Newman-Kuel's procedure.

Parameter	Ridge top	Upper slope	Lower slope/hill	Streamside	p*
Elevation (m)	541.8 ± 27.2^{a}	509.3 ± 36.6^{a}	70.1 ± 6.1^{b}	231.9 ± 15.9^{b}	0.0001
Species richness	19.7 ± 0.9^{a}	34.0 ± 2.5^{b}	38.1 ± 1.9^{b}	39.1 ± 1.9^{b}	0.0001
Overstory cover (%)	33.4 ± 8.9^{a}	$82.5~\pm~4.5^{\rm b}$	82.3 ± 2.6^{b}	89.1 ± 2.3^{b}	0.0001
Understory cover (%)	55.4 ± 7.3^{a}	45.9 ± 5.8^{a}	21.8 ± 3.8^{b}	23.0 ± 2.7^{b}	0.0001
Shrub cover (%)	19.8 ± 2.9^{a}	$48.4~\pm~4.4^{\rm b}$	42.7 ± 3.7^{b}	44.4 ± 3.3^{b}	0.0001
Herbaceous cover (%)	30.0 ± 3.0^{a}	$46.1\pm4.2^{\rm b}$	52.7 ± 3.3^{b}	28.5 ± 3.1^{a}	0.0001

*, Probability of error for rejecting Ho in ANOVA.



Figure 2. P. densiflora (Korean red pine) forests in four landscape positions: ridge top (top left), upper slope (top right), lower slope/hill (bottom left), and streamside (bottom right).

cover, while no statistical differences were found among the other positions.

Woody Vegetation

P. densiflora dominated the woody vegetation at all landscape positions. Quercus mongolica was the subdominant woody species on the ridge top, the upper slope, and the lower slope/hill, while Populus maximowiczii was sub-dominant at the streamside. Quercus serrata and Robinia pseudoacacia were also major woody species on the upper slope and the lower slope/hill, respectively (Table 2). In the understory layer, P. densiflora constituted 89% of the stems on the ridge top, but its relative importance decreased to 16%, 28%, and 33% on the upper slope, lower slope/hill, and streamside, respectively. Quercus mongolica had the highest share of the understory (45%) on the upper slope but was lowest (1%) at streamside. Other species (e.g., Robinia pseudoacacia and P. maximowiczii) comprised a larger share of the understory stems than P. densiflora and Q. mongolica in the lower slope/hill and streamside plots (Fig. 3). Based on the DCA for 14 woody species (Fig. 4), the eigen-values of the total variation, the first, and the second axes were 1.96, 0.36, and 0.21, respectively. On the first axis, the dominance of R. pseudoacacia and Castanea crenata increased, while *P. maximowiczii* and *Styrax* spp. decreased, from left to right. *Betula schmidtii* and *Q. mongolica* increased from bottom to top, while *Rhus trichocarpa* and *Q. serrata* increased from top to bottom, on the second axis. More than 50% of the *P. densiflora* stems were less than 25 years old on the ridge top, whereas approximately 55% were older than 51 years on the upper slope. Nearly 60% were between 26 and 50 years old on the lower slope/hill and at streamside. Fewer large stems (>51 years old) occurred in the streamside plots (Fig. 5).

Herbaceous Vegetation

Table 3 lists the major herbaceous species that occurred in 30% or more of the plots at each landscape position. *Spodiopogon sibiricus* and *Carex humilis* var. *nana* were dominant at all positions. *Chrysanthemum zawadskii* sub-dominated along the ridge top and the upper slope, while *Artemisia keiskeana* and *Phragmites japonica* were subdominants in the lower slope/ hill and streamside plots, respectively. The DCA for 28 herbaceous species is shown in Figure 6. Eigenvalues for total variation, and the first and second axes were 2.20, 0.40, and 0.20, respectively. *P. japonica* and *Oplismenus undulatifolius* increased their dominance from left to right, i.e., in the reverse direction

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Species	Basal Area (m² ha ⁻¹)	Density (stems ha ⁻¹)	
Ridge top (n = 25)			
Pinus densiflora Sieb. et Zucc.	35.4 ± 3.5	2,388 ± 396	
Quercus mongolica Fischer	0.6 ± 0.3	1,253 ± 572	
Upper slope (n = 22)			
Pinus densiflora Sieb. et Zucc.	49.2 ± 4.9	958 ± 167	
Quercus mongolica Fischer	2.5 ± 0.7	$3,263 \pm 666$	
Quercus serrata Thunb.	2.0 ± 0.7	362 ± 151	
Betula schmidtii Regel	0.5 ± 0.2	$106~\pm~39$	
Prunus sargentii Rehder	0.5 ± 0.1	89 ± 25	
Fraxinus rhynchophylla Hance	$0.2~\pm~0.1$	98 ± 33	
Acer pseudo-sieboldianum (Pax) Komar.	0.2 ± 0.1	85 ± 22	
Styrax obassia Sieb. et Zucc.	0.1 ± 0.1	54 ± 15	
Lower slope/hill (n = 37)			
Pinus densiflora Sieb. et Zucc.	$44.9~\pm~2.0$	1,727 ± 162	
Quercus variabilis Blume	1.7 ± 0.2	150 ± 25	
Robinia pseudoacacia L.	$0.4~\pm~0.1$	$299~\pm~65$	
Castanea crenata Sieb. et Zucc.	0.2 ± 0.1	$117~\pm~35$	
Rhus trichocarpa Miquel	0.2 ± 0.1	$112~\pm~25$	
Quercus mongolica Fischer	0.1	219 ± 90	
Streamside ($n = 43$)			
Pinus densiflora Sieb. et Zucc.	33.6 ± 1.9	1,290 ± 91	
Populus maximowiczii A. Henry	4.1 ± 0.5	$141~\pm~34$	
Fraxinus rhynchophylla Hance	0.6 ± 0.1	140 ± 22	
Prunus sargentii Rehder	$0.4~\pm~0.1$	76 ± 7	
<i>Styrax japonica</i> Sieb. et Zucc.	0.3 ± 0.1	98 ± 18	
Styrax obassia Sieb. et Zucc.	0.2 ± 0.1	98 ± 24	

Table 2. Basal areas (means \pm standard errors) and densities (means \pm standard errors) of major tree species (>20% frequency) on *P. densiflora* forests in four landscape positions at Mt. Seorak, Korea.

for Sanguisorba hakusanensis var. coreana and Aster ciliosus, on the first axis. On the second axis, Arundinella hirta and S. hakusanensis increased their dominance from bottom to top, in the reverse of Disporum smilacinum and Smilax nipponica var. manshurica.

Soil Characteristics

The ridge top had the coarsest soil texture (>60% gravel), while the streamside and upper slopes had the highest contents of sand (>80%) and silt-clay (>50%), respectively. Moisture retention capacity was highest on the upper slope, followed in order by the lower slope/hill, ridge top, and streamside (Table 4). Soil along the streamside was the most acidic; soil pH

did not differ significantly among the other positions. Levels of organic matter (OM) were highest on the lower slope/hill and lowest at streamside, while EC and CEC were higher for the upper and lower slope/ hill than for the ridge top and streamside. Differences in CEC between the upper slope and lower slope/hill and between the streamside and ridge top were not statistically significant. Likewise, EC from the streamside and the ridge top was not different significantly. Although N and P contents were significantly higher on the upper slope than at the other positions, no statistically significant difference was found among the other three locations. Ca and K levels were lower along the streamside than at the other positions, but no significant difference was found among the latter group. Mg contents were higher on the upper and lower slopes/hills than at the ridge top or along the streamside, but those concentrations were not statistically different between ridge top and streamside (Table 5).

DISCUSSION

General Physiognomy

Numerous abiotic factors, such as climate, topography, soil, and land-use, contribute to the composition and dynamics of *P. densiflora* forests (Toyohara, 1984; Lee and Lee, 1989; Rim et al., 1991). Song and Kim (1993) and Lee (1995) have reported that this species can tolerate xeric soils, a coarse texture, and low retentions of moisture and nutrients. Therefore, normally inhospitable conditions, e.g., xeric and infertile soils, can provide an opportunity for stress-tolerant P. densiflora by reducing competition with competitive but stress-intolerant species (Grime, 1977). The higher percentages of gravel/sand (Table 4) and generally low fertility (Table 5) from the soils in our P. densiflora-dominated plots are similar to those reported by Song and Kim (1993) and Lee (1995). Reductions in the understory and herbaceous cover along the streamside and on the lower slope/hill (Table 1) were likely caused by periodic flooding and human disturbance (e.g., foot traffic and brush removal), respectively.

Ridge Top

The thin and xeric soil along the ridge top probably resulted in low species richness (Table 1), thereby permitting the sporadic occurrence of drought-tolerant species such as *A. hirta*, *A. ciliosus*, and *S. hakusanen*-



Figure 3. Seedling frequencies at four landscape positions for *P. densiflora* forests at Mt. Seorak, Korea. Pine, *P. densiflora*; Qm, *Q. mongolica*; Qsp, *Quercus* spp; Other, other woody plants.



Figure 4. DCA ordination of woody vegetation from 127 plots with 14 species (>20% frequency) in four landscape positions of *P. densiflora* forests at Mt. Seorak, Korea. Ridge top, upper slope, lower slope/hill, and streamside plots are indicated by 'T', 'U', 'L', and 'S', respectively.

sis (Table 3; Fig. 5; Lee, 1996). The soil at that position was also inhospitable to tree species, with even the drought-tolerant *P. densiflora* showing stunted growth (Fig. 2) in the thin, coarse, and xeric soil (Table 4). This result is consistent with that reported by Lee and Hong (2004). The high density (Table 2) of young seedlings (<25 years old in Fig. 5) suggests their con-

tinuous recruitment in the exposed soil. Such recruitments plus very little competition with other tree species in the open landscape may have enabled *P. densiflora* to maintain its dominance on the ridges and rock outcroppings. Therefore, despite its noticeable dominance, *Q. mongolica* probably would not replace *P. densiflora*, mainly due to its inability to tolerate a xeric environment (Lee and Lee, 2003) at the ridge top.

Upper Slope

Most *P. densiflora* stands occurred on south or south-west facing slopes, which were exposed to direct solar radiation. Soil on the upper slope was relatively fertile, with high moisture retention capacity (Table 4, 5). The greater fertility and moisture retention there was likely due to the accumulation of organic matter (Kim, 1989), mostly from litter decomposition of deciduous trees. Kim and Chang (1967) and Park and Lee (1981) have reported relatively high production of deciduous litter at high elevations near our study sites. Because of their low lignin and cellulose contents (Barbour et al., 1999), deciduous litters are more readily decomposed than coniferous needles (Cha et al., 1969; Salamanca et al., 2003). These fertile soils with high moisture retention were conducive



Figure 5. Age distribution of *P. densiflora* populations in four landscape positions at Mt. Seorak, Korea.

Table 3. Frequency and dominance of major herbaceous species (>30% frequency) on P. densiflora forests in four landsca	ape
positions at Mt. Seorak, Korea.	

Species	Frequency (%)	Dominance
Ridge top (n = 25)		
Spodiopogon sibiricus Trinius	100.0	7.62
Carex humilis var. nana (Lev. et Van.) Ohwi	92.0	9.51
Chrysanthemum zawadskii Herbich	84.0	3.02
Artemisia keiskeana Miquel	64.0	1.24
Polygonatum odoratum var. pluriflorum (Miq.) Ohwi	60.0	0.45
Peucedanum terebinthaceum (Fischer) Fischer	56.0	0.06
<i>Viola orientalis</i> (Maxim.) W. Becker	56.0	0.06
Arundinella hirta (Thunb.) C. Tanaka	52.0	1.84
Atractylis japonica Koidz.	48.0	0.05
Aster ciliosus Kitamura	48.0	0.05
Patrinia saniculaefolia Hemsley	44.0	0.63
Melica onoei Fr. & Sav.	32.0	0.82
Sanguisorba hakusanensis var. coreana Hara	32.0	0.73
Calamagrostis arundinacea (L.) Roth	32.0	0.23
Upper slope (n = 22)		
Spodiopogon sibiricus Trinius	95.5	6.50
Carex humilis var. nana (Lev. et Van.) Ohwi	81.8	8.98
Chrysanthemum zawadskii Herbich	68.2	2.30
Peucedanum terebinthaceum (Fischer) Fischer	63.6	0.73
Melampyrum setaceum var. nakaianum (Tuyama) Yamazaki	59.1	1.52
Artemisia keiskeana Miquel	59.1	1.40
Polygonatum odoratum var. pluriflorum (Miq.) Ohwi	54.5	1.29
Atractylis japonica Koidz.	50.0	0.05
Solidago virga-aurea var. asiatica Nakai	40.9	0.04
Melica onoei Fr. & Sav.	31.8	0.48

Table 3.	Continued
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Species	Frequency (%)	Dominance
Lower slope/hill (n = 37)		
Spodiopogon sibiricus Trinius	86.5	9.21
Artemisia keiskeana Miquel	81.1	9.74
Patrinia villosa (Thunb.) Jussieu	75.7	1.00
Carex humilis var. nana (Lev. et Van.) Ohwi	73.0	11.96
Polygonatum odoratum var. pluriflorum (Miq.) Ohwi	73.0	1.74
Aster scaber Thunb.	64.9	0.20
Potentilla freyniana Bornm.	56.8	0.98
Chrysanthemum zawadskii Herbich	51.4	0.85
Smilax nipponica var. manshurica (Kitagawa) Kitagawa	51.4	0.32
Atractylis japonica Koidz.	48.6	0.58
Disporum smilacinum A. Gray	43.2	3.80
Viola orientalis (Maxim.) W. Becker	43.2	0.91
Melica onoei Fr. & Sav.	40.5	0.84
<i>Dioscorea japonica</i> Thunb.	40.5	0.44
Solidago virga-aurea var. asiatica Nakai	40.5	0.04
Pteridium aquilinum var. latiusculum (Desv.) Und.	37.8	1.24
Melampyrum setaceum var. nakaianum (Tuyama) Yamazaki	35.1	4.20
Carex lanceolata Boott	32.4	1.03
Peucedanum terebinthaceum (Fischer) Fischer	32.4	0.16
Streamside (n = 43)		
Carex humilis var. nana (Lev. et Van.) Ohwi	81.4	4.46
Spodiopogon sibiricus Trinius	79.1	2.89
Phragmites japonica Steud.	67.4	3.70
Calamagrostis arundinacea (L.) Roth	65.1	1.66
Oplismenus undulatifolius (And.) Beauv.	60.5	1.49
Isodon excisus (Maxim.) Kudo	62.8	0.29
Melica onoei Fr. & Sav.	48.8	0.73
Carex lanceolata Boott	46.5	0.68
Solidago virga-aurea var. asiatica Nakai	41.9	0.52
Carex siderosticta Hance	37.2	0.04
Peucedanum terebinthaceum (Fischer) Fischer	30.2	0.14

to growth of *P. densiflora* and other tree species on the upper slope (Table 2). Increased availability of nutrients and soil moisture may favor competitive species (e.g., *Q. mongolica* and *Q. serrata*) over stress-tolerant species (e.g., *P. densiflora*) (Grime, 1977). Such transitions from coniferous to deciduous forest have been documented elsewhere (e.g., Smith and Linnartz, 1980; Yim and Baik, 1985; Lee, 1989; Williams and Johnson, 1990; Lee, 1993; Hong et al., 1995; Hong, 1998, 2004; Lee and Hong, 2004). In fact, the low frequency of young *P. densiflora* (<50 years old, Fig. 5) combined with the increased dominance of *Quercus* (Table 2, Fig. 3) in the understory layer indicates a suc-

cession trajectory to a *Quercus* forest in the upper slope. Moreover, this transition would likely be facilitated by dieback in *P. densiflora* forests because of infestation by pests such as the pine gall midge (Lee, 1989; Fujihara, 1996; Fujihara et al., 2002).

Lower Slope/Hill

Soils on the lower slope/hill had relatively high organic matter, nutrient contents, and moisture retention capacity, which may have made this position more hospitable to plant growth, including pine, than those on the ridge top and upper slope. However,

Table 4. Physical characteristics of *P. densiflora* forest soils in four landscape positions at Mt. Seorak, Korea. Each characteristic is expressed as a mean \pm SE. Values followed by the same letter within a column are not statistically different at p = 0.05, based on Newman-Kuel's procedure.

Parameter	Ridge top $(n = 9)$	Upper slope $(n = 12)$	Lower slope/ hill (n = 8)	Streamside $(n = 11)$	p*
Gravel (%)	64.48 ± 4.15^{a}	$43.03 \pm 3.59^{ m b}$	$29.27 \pm 5.13^{\circ}$	16.07 ± 3.32^{d}	0.0001
Sand (%)	34.65 ± 4.02^{a}	$54.37 \pm 3.49^{ m b}$	$68.84 \pm 5.02^{\circ}$	83.40 ± 3.29^{d}	0.0001
Silt & Clay (%)	0.87 ± 0.25^{a}	$2.60\pm0.44^{\rm b}$	$1.90 \pm 0.38^{a,b}$	$0.54 \pm 0.13^{\circ}$	0.0001
Moisture retention capacity	41.25 ± 2.91^{a}	52.81 ± 2.68^{b}	$48.22\pm2.52^{a,b}$	$29.06 \pm 2.00^{\circ}$	0.0001

*, Probability of error for rejecting Ho in ANOVA.

Table 5. Chemical characteristics of *P. densiflora* forest soils in four landscape positions at Mt. Seorak, Korea. Each characteristic is expressed as a mean \pm SE. Values followed by the same letter within a column are not statistically different at p = 0.05, based on Newman-Kuel's procedure.

Parameter	Ridge top (n = 9)	Upper slope $(n = 12)$	Lower slope/ hill (n = 8)	Streamside $(n = 11)$	p*
pН	5.06 ± 0.10^{a}	5.09 ± 0.12^{a}	5.13 ± 0.07^{a}	5.64 ± 0.09^{b}	0.0002
OM ^A (%)	2.65 ± 0.37^{a}	$4.90\pm1.04^{ m b}$	$7.23\pm0.93^\circ$	$1.38 \pm 0.18^{\mathrm{a,b}}$	0.0001
EC ^B (ms cm ⁻¹)	0.15 ± 0.02^{a}	$0.22 \pm 0.02^{\rm b}$	$0.22\pm0.02^{\rm b}$	0.09 ± 0.01^{a}	0.0001
CEC ^C (meq100 g ⁻¹)	4.69 ± 1.16^{a}	$8.77\pm0.99^{ m b}$	$9.22 \pm 1.15^{ m b}$	3.08 ± 0.46^{a}	0.0001
P (ppm)	6.22 ± 0.55^{a}	12.75 ± 1.79^{b}	7.50 ± 2.20^{a}	7.00 ± 0.42^{a}	0.0038
N (%)	0.08 ± 0.02^{a}	$0.19\pm0.04^{ m b}$	0.09 ± 0.02^{a}	0.06 ± 0.02^{a}	0.0022
K (ppm)	$0.11~\pm~0.05^{\scriptscriptstyle \rm d}$	0.16 ± 0.02^{a}	0.21 ± 0.04^{a}	$0.03\pm0.01^{ m b}$	0.0005
Ca (ppm)	0.15 ± 0.03^{a}	$0.64\pm0.19^{ m b}$	$0.40\pm0.12^{ m b}$	$0.49 \pm 0.08^{\rm b}$	0.0666
Mg (ppm)	$0.06\pm0.01^{\rm a}$	0.17 ± 0.03^{b}	$0.22\pm0.04^{\rm b}$	$0.08 \pm 0.01^{\circ}$	0.0002

*, Probability of error for rejecting Ho in ANOVA.

OM^A, organic matter; EC^B, electrical conductivity; CEC^C, cation exchange capacity.



Figure 6. DCA ordination of herbaceous vegetation from 127 plots with 28 species (>30% frequency) in four landscape positions of *P. densiflora* forests at Mt. Seorak, Korea. Ridge top, upper slope, lower slope/hill, and streamside plots are indicated by 'T', 'U', 'L', and 'S', respectively.

due to easy access at these lower elevations, this position historically has been subjected to anthropogenic disturbances, e.g., forest thinning, brush removal, and the gathering of fuel wood (Kamada et al., 1987, 1991; Hong et al., 1995; Hong, 1998), as well as artificial plantings for cash crops or erosion control (Lee et al., 2004) and more recent artificial management pursued in the name of the "forest tending practices movement" by the government. Nevertheless, when left to natural processes without active human intervention, reductions of the understory cover in a pine forest can also result from rapid growth by competitive tree species.

In our study area, however, artificial interferences previously described were the greater influence, such that understory coverage was diminished on the lower slope/hill (Table 1) and was comprised instead by a mixture of herbaceous species typically found under the forest canopy (e.g., *D. smilacinum* and *S. nipponica*), as well as forest-edge species (e.g., *R. multiflora* and *D. japonica*), and introduced species (e.g., *R. pseudoacacia* and *C. crenata*) (Table 2, 3). In particular, the harvesting of *P. densiflora* stands for fuel wood or commercial timber until the early part of the

20th Century (Lee et al., 2001) was likely responsible for the low frequency of mature P. densiflora stands (>51 years old). In contrast, widespread use of fossil fuels plus governmentally imposed restrictions later in that century discouraged fuel wood gathering (Hong et al., 1995; Hong, 1998; Lee et al., 2001), thus allowing the Korean red pine seedlings to grow for 26 to 50 years on the lower slope/hill (Fig. 5). Decreases in those artificial disturbances, however, also encouraged the concurrent regrowth of deciduous tree species, including Quercus, in the understory layer (Fig. 3). Establishment of deciduous trees increases canopy closure and litter production, diminishing the level of solar radiation reaching the forest floor (Williams, 1989). That decline in radiation then discourages the recruitment and growth of P. densiflora seedlings. Indeed, pine seedlings occurred only in plots with <20% understory cover, i.e., those locations where gaps were created by pine gall midge infestation or human activities. Therefore, the current dominance by P. densiflora could possibly be replaced by Quercus on the lower slope/hill. However, the strong likelihood for disturbance (from either humans or pests) makes this an uncertain prediction.

Streamside

Although the riparian soils received a constant water supply from adjacent streams, their contents of silt and clay were the lowest among the four landscape positions, resulting in poor moisture retention capacity. These low amounts may have been due to periodic upstream inputs of sand and gravel as well as the erosion of silt and clay by flash floods during the summer monsoon months. Floods also extensively destroyed young P. densiflora seedlings at that site (Fig. 3). Drastic disturbances (such as flash flooding) may create ample spaces for the establishment of new species (Hibbs, 1982). McVean (1963) has noted that an open landscape with plentiful solar radiation and well-drained soil in riparian zones can provide a favorable environment for pine seedlings. Oh (1970) has demonstrated that riparian habitats create temporary 'safe sites' for anemochory species, e.g., P. densiflora, P. maximowiczii, and P. japonica (Kim and Yim, 1991). The age of our P. densiflora stands (26 to 50 vears old) suggests their establishment likely began 50 years ago, following a major disturbance such as a flood (Fig. 5). Nevertheless, during the past 20 to 30 years, periodic floods seemed to wash away significant numbers of P. densiflora seedlings. In addition, the extensive canopy closure (Table 1) discouraged the survival and growth of new pine recruits, such that nearly 25% of those 20- to 35-year-old pine trees (6 to 15 cm DBH) were dead on our sites (Chun, 2001). A few pioneer species -- *P. maximowiczii, Fraxinus rhynchophylla*, and *Prunus sargentii* -- had become widely established in those created gaps. However, as with *P. densiflora*, those species are not shade-tolerant under a dense canopy, and can be damaged or killed by periodic floods. Because those pioneer tree species could not grow tall enough to replace the *P. densiflora* canopy, the pines probably would continue their dominance in the canopy layer. In fact, the high density and basal area of *P. densiflora* (Table 2) supports our prediction.

Management Implications

Conservation of Korean red pine forest is a priority in natural resource management because that species is so highly valued by Korean people (Lee et al., 1983; Son and Hwang, 1990; Youn and Kim, 1992; KFRI, 1999). Our results suggest that the P. densiflora stands on the upper and lower slopes and hills will likely decline in the near future because of either natural succession by oak species or from human disturbance, or both. The major threats to seedlings of that species include canopy closure and invasions by other woody species on the lower slopes and hills. However, prescribed thinning and brush removal could easily improve the environment for P. densiflora by both opening the canopy for sunlight and reducing competition with other woody species. Meanwhile, the conservation of P. densiflora forests on upper slopes is a philosophical dilemma. Converting from shade-intolerant Pinus to shade-tolerant Quercus forest is often considered as a process of "natural" succession (Smith and Linnartz, 1980; Yim and Baik, 1985; Lee, 1989; Williams and Johnson, 1990; Lee, 1993; Hong et al., 1995; Hong, 1998; Lee and Hong, 2004; Hong, 2004). Furthermore, Nishida (1978; as cited by Hong, 1998) has noted the replacement of deciduous species by pine forest approximately 3000 years ago, mainly due to human intervention (e.g., slash-and-burn agriculture and fuel wood collection). Since then, any natural succession from Pinus to Quercus has been arrested artificially for human benefits (Hong et al., 1995; Hong, 1998). Therefore, the conservation of pine forest might be considered simply a further arrest of "natural" succession (from Pinus to Quercus), based on our traditional human values. We are unable to reach a conclusion whether to allow a 'natural' process for replacing pine by oak species, or to artificially interrupt this 'natural' succession in order to preserve the current *P. densiflora* forests. Our report here is not intended to influence the making of management decisions, or to suggest that, for cultural value, *Pinus* forests be conserved by suppressing natural succession to *Quercus* forests, or vice versa in order to gain natural values. However, we hope that our data will serve as guidance in managing these *P. densiflora* forests.

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