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Macronutrient input from pollen in two regenerating pine stands in southeast Korea

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This study examined macronutrient input from pollen in two naturally regenerating pine stands in southeast Korea. Durham gravity pollen collectors were used to measure pine pollen deposition and the macronutrients in the collected pine pollen were analyzed. In 1998, pine pollen deposition began just before 18 April and lasted for approximately 2 weeks. Total pine pollen deposition differed between the two sampling sites; 27.5 kg ha^{-1} was collected from the mature stand and 17.7 kg ha^{-1} was collected from the young stand. The values for nutrient deposition from pine pollen are 549 g ha^{-1} N, 78 g ha^{-1} P, 240 g ha^{-1} K, 45 g ha^{-1} S and 22 g ha^{-1} Mg at the mature stand and 353 g ha^{-1} N, 51 g ha^{-1} P, 151 g ha^{-1} K, 27 g ha^{-1} S and 14 g ha^{-1} Mg at the young stand, suggesting that nutrients from pine pollen contribute to forest nutrient cycling. The pine pollen deposition values obtained from our study (17.7–27.5 kg^{-1} ha^{-1} $year^{-1}$) are approximately 1/115–180-fold that of pine litterfall in Korea. If we take pollen nutrients into account, the contribution rate of pollen to the annual nutrient input is very high in our study (N 1/30, P 1/5, K 1/9 that of litterfall). Macronutrient deposition from pine pollen is concentrated temporally in spring. Although the annual contribution of nutrient mass by pollen is small compared to that of litterfall, the rapid turnover rate of pollen nutrients combined with episodic deposition suggests that pollen may play a disproportionate role in temperate pine forest nutrient cycling.

Key words: macronutrients; nutrient cycling; phenology; pine, pollen.

INTRODUCTION

Considerable quantities of pine pollen are deposited over a short period in spring and/or summer in many forest ecosystems (Saito & Takeoka 1985; Sekiguchi *et al*. 1986; Doskey & Ugoagwu 1989; Lee *et al*. 1996a, b). Because pollen grains decompose rapidly and have high macronutrient concentrations, pollen rain may be an important component of nutrient dynamics in natural terrestrial and aquatic ecosystems (Stark 1972, 1973). Few studies provide insights into the role of pollen in forest nutrient cycling. Doskey and Ugoagwu (1989) found that pine pollen was an important source of macronutrients in oligotrophic lakes in northern Wisconsin. Stark (1972) suggested that pollen allows fungi to obtain sufficient N, P and other elements to complete litter decay, which in turn releases other nutrients that are needed for tree growth.

Despite these studies, pollen has generally been overlooked in studies of forest nutrient cycling. Foster and Morrison (1976) did not consider pollen in their model of nutrient dynamics in boreal jack pine forests, despite the fact that jack pines (*Pinus banksiana*) produce considerable quantities of pollen annually. Although the input of macronutrients from pollen was found to have a trigger effect on nutrient dynamics by promoting litter decomposition and increasing nutrient uptake rates (Stark 1972), little information is available on the quantities of pine pollen deposition in mixed temperate forests (Kim 1985; Saito & Takeoka 1985; Sekiguchi *et al*. 1986).

In this study, we examined atmospheric macronutrient input from pine pollen in a mixed tem-

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perate forest in southeast Korea. Annual pine pollen deposition was determined in mature and young regenerating pine stands. We estimated pollen macronutrient fluxes based on the measured pollen deposition rates and macronutrient contents and discuss the possible importance of pine pollen to the cycling of macronutrients in temperate pine forests.

METHODS

Study sites

The study area is located in southeast Korea, approximately 10 km west of the city of Taegu (35°51′ N, 128°29′ E). The size of the mature pine stand is 2.5 ha and the size of the young pine stand is 1.2 ha. The mean elevation is approximately 100 m a.s.l. Both stands lie on the southeast facing slope of a small mountain. The climate is temperate and the growing season extends from early March to early November. Mean annual precipitation is 979 mm, mean annual temperature is 12.6°C, and the prevailing winds are from the northwest in winter and from the south in summer. More than half of the annual precipitation occurs in summer (June–August) and winters tend to be dry and cold, reflecting a typical continental weather pattern. Weather statistics were based on data from the Taegu weather station, approximately 11 km east of the study sites.

Vegetation survey

Forest stand information along the two stands (approximately 100 m apart) was determined using the point-centered quarter method (Mueller-Dombois & Ellenberg 1974). Ten points were located at 10-m intervals along each stand, and at each point the distance to, and basal area of, the nearest tree (>2.5 cm in diameter and >2 m in height) in each of four quadrats were measured. A total of 80 trees and tall shrubs were enumerated. The study area lies on granitic rocks. Soils are generally thin with a weakly developed top soil profile. The region lies within the Sino-Japanese floristic section (Good 1953). Within the study area, Japanese red pine (*Pinus densiflora* S. et Z.) and pitch pine (*Pinus rigida* Miller) are codominant on the poorly developed soils. Black locust (*Robinia pseudoacacia* L.) grows at the edge of the forest. *Pinus densiflora* trees are 8–12 m and 4–7 m high with mean diameters of 14.5 cm and 8 cm at breast height in the mature and young stands, respectively. The mean age of *P. densiflora* trees is 45 years and 18 years in the mature and young stands, respectively ($n = 10$ at each stand).

Pollen deposition

Pollen deposition in the two pine stands was determined from sampling undertaken from 18 April to 1 May 1998 and only *Pinus* pollen deposition was determined. Raw data and voucher slides from the 1998 field season are available from Dr E. J. Lee, School of Biological Sciences, Seoul National University. Twelve gravity pollen collectors were set up in each stand to collect the pine pollen. Collectors were located approximately 10 m apart from the east to the west side of the stands. To minimize forest-trail edge effect, collectors were randomly located between 5 and 12 m from the narrow trail. Pollen collectors were examined at 24-h intervals. Direct daily observations of collected catkins and male cones were done to determine the timing of pine pollen release.

Durham (1946) gravity pollen collectors were employed in this study. These collectors were selected in preference to mechanical samplers for reasons of: (i) cost; (ii) inaccessibility to power for mechanical samplers; (iii) the need for uninterrupted data correction; and (iv) the likelihood of animal damage. This sampling device was approved by the National Pollen Survey Committee as a standard method for atmospheric pollen deposition. A Durham pollen collector consists of two horizontal disks (23 cm in diameter, 15 cm apart), with the lower disk located 9 cm from ground level. A standard 2 cm × 8 cm glass slide covered with a thin film of petroleum jelly was placed on the lower disk to collect pollen. Slides were exposed for 24 h. Slides were kept in a tightly sealed slide box before and following exposure to prevent contamination, and were examined under a stereomicroscope (100× magnification) to identify pollen and estimate pollen numbers. Pollen deposition was determined by counting all grains within a randomly selected 0.25 cm^2. The amount of pollen rain was expressed as the number of pol-

len grains per square centimeter. The mean volume of 50 air-dried pollen grains was determined by measuring the (a) length, (b) width and (c) depth of air-dried pollen and then using the equation $4/3\pi abc$. Pollen mass was determined from the mean volume estimates and the measured mass of 50 ml of air-dried pollen. In a 50 ml pollen container, we estimated using a geometrical calculation that 52.2% of the volume was filled by pollen and 47.8% was empty space. Individual grain mass was then obtained from the known mass and volume of 50 ml air-dried pollen. Pollen counts and mass were used to determine annual pollen deposition.

Pollen macronutrient analysis

Three replicate samples of 1 g of air-dried *P. densiflora* and *P. rigida* pollen were collected and fresh pollen samples were obtained in the field by gently shaking a branch (containing male cones) to which a plastic bag had been attached. Air-dried pollen samples were analyzed for N, P, K, S and Mg at the National Instrumentation Center for Environmental Management. Total N was determined using the Kjeldahl digestion method (Bremner 1960) and total P, S, K and Mg were determined using an inductively coupled plasma emission spectrometer (ICPS-1000IV, Shimadzu, Japan) after acid digestion (Sparks 1996).

RESULTS

Tree frequencies and basal area values from the study stands are summarized in Table 1. The common tree species are *P. densiflora*, *P. rigida* and *R. pseudoacacia* in descending order. *Pinus densiflora* accounted for 64% of the total basal area in the mature pine stand and 86% in the young pine stand. *Pinus rigida* was codominant (with *P. densiflora*) in the mature pine stand and *R. pseudoacacia* accounted for 14% in the young pine stand.

Pine pollen deposition differed between the mature and the young pine stands and averaged 13 480 grains cm^{-2} (27.5 kg ha^{-1}) in the mature pine stand and 8660 grains cm^{-2} (17.7 kg ha^{-1}) in the young pine stand during April–May 1998 (Table 2).

Although the total basal area of the mature pine stand was 20-fold higher than that of the young pine stand, pine pollen deposition was only 1.5-fold higher in the mature pine stand.

In 1998, pollen deposition began just before 18 April and lasted for approximately 2 weeks (Table 3; Fig. 1). Two species of pine (*P. densiflora* and *P. rigida*) differed in the timing of pollen release, with *P. rigida* beginning pollen release 2 days earlier than *P. densiflora*. However, the shape and size of pollen from these species are very similar, thus no attempt was made to distinguish

Table 2 Pollen deposition in two regenerating pine stands in southeast Korea, 1998

Species	No. grains cm^{-2}	Deposition (g ha^{-1})
Mature stand		
Pinus densiflora	13 479 ± 2318 (10 134–16 493)	27 544
Young stand		
Pinus densiflora	8660 ± 475 (8271–9593)	17 696

Values are mean ± 1 SD (range).

Table 1 Forest composition in two regenerating pine stands in southeast Korea (based on $n = 40$ trees in each stand)

Species	Proportion of individuals (%)	Total basal area (cm^2 ha^{-1})	Relative basal area (%)
Mature stand			
Pinus densiflora	70.0	28 306	64.4
Pinus rigida	30.0	15 647	35.6
Young stand			
Pinus densiflora	87.5	1750	86.2
Robinia pseudoacacia	12.5	279	13.8

Table 3 Mean daily temperature, precipitation, duration of sunshine and pine pollen deposition in southeast Korea in 1998

Date	Temperature (°C)	Precipication (mm)	Sunshine (h)	Pollen deposition (grains cm^{-2} day^{-1}) Mature stand	Young stand
18 April	15.8		10.3	636	317
19 April	19.9		10.8	1484	740
20 April	21.7		10.5	2808	1388
21 April	20.6	0.0	1.2	2139	911
22 April	21.4	0.0	0.7	430	183
23 April	22.3	25.9	3.7	688	293
24 April	23.6		5.2	1449	1622
25 April	13.4	2.4	0.9	828	799
26 April	14.4		4.9	889	357
27 April	17.4	0.1	9.9	543	458
28 April	19.8		11.8	614	604
29 April	19.3		9.2	564	567
30 April	18.3		6.8	320	322
1 May	17.0	2.2	0.0	86	100

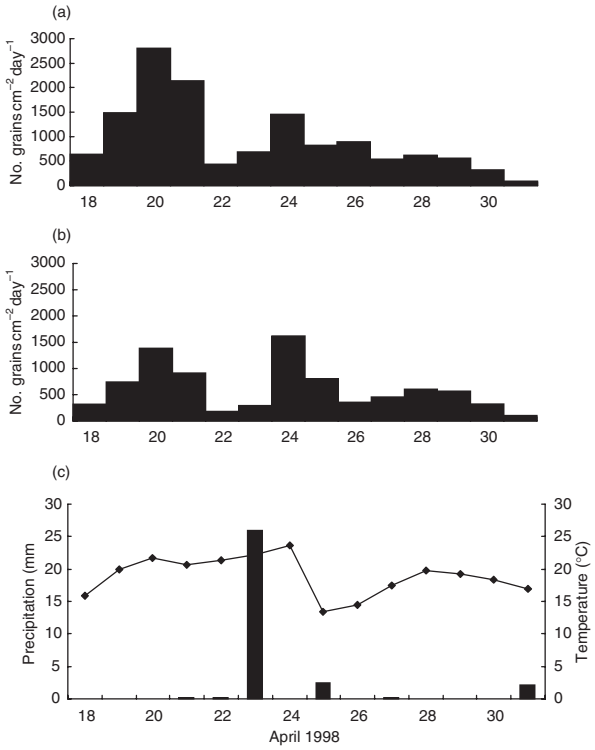

Fig. 1. Mean pine pollen deposition (grains cm^{-2} day^{-1}) in (a) a mature pine stand and (b) a young pine stand and (c) the daily temperature (◆) and precipitation (■) in southeast Korea in 1998.

between these species in counting. Peak periods of pine pollen deposition occurred on 20 April in the mature pine stand (2808 grains cm^{-2} day^{-1}) and 24 April in the young pine stand (1622 grains cm^{-2} day^{-1}). Rainfall (approximately 31 mm in total) occurred on 21, 22, 23 and 25 April and on 1 May in the study area. The mean daily temperature rose steadily from 18 April (15.8°C) to 24 April (23.6°C) and dropped suddenly to 13.4°C on 25 April.

Nitrogen is the most abundant macronutrient in *P. densiflora* and *P. rigida* pollen, followed by K, P, Mg and S (Table 4). Macronutrient concentrations showed little variation between the species; however, sulfur did vary between *P. densiflora* and *P. rigida* pollen.

The pollen length of *P. rigida* (47.4 μm) was slightly larger than that of *P. densiflora* (43.9 μm). To determine macronutrient input we took the value of *P. densiflora* because it was the dominant pollen donor in the study area. The estimated total macronutrient deposition in the two stands is represented in Table 5. Total macronutrient deposition was higher in the mature pine stand than in the young pine stand. Nutrient inputs from pine pollen were approximately 549 g N ha^{-1}, 240 g K ha^{-1} and 78 g P ha^{-1} in the mature pine stand and one-third lower in the young pine stand.

Table 4 Macronutrient concentrations in pine pollen collected from the study area and other comparable sites

Species	N	P	K	S	Mg
Pinus densiflora	19.95 ± 0.51	2.90 ± 0.03	8.58 ± 0.32	1.52 ± 0.03	0.78 ± 0.04
Pinus rigida	22.54 ± 1.97	2.74 ± 0.04	9.32 ± 0.95	1.81 ± 0.03	0.85 ± 0.09
Pinus banksiana[†]	20.30 ± 0.06	2.90 ± 0.12	8.30 ± 0.58	0.70 ± 0.10	0.70 ± 0.06

[†]Pollen collected from Manitoba, Canada. Data from Lee *et al*. (1996b).
Values are mg per gram of pollen ± 1 SD ($n = 3$).

Table 5 Estimated macronutrient deposition (g ha^{-1}) by pine pollen in the two pine stands

Stand	N	P	K	S	Mg
Mature stand	548.6	77.6	240.4	45.3	22.1
Young stand	353.1	51.3	151.9	26.9	13.8

DISCUSSION

Mean pine pollen deposition was estimated to be approximately 27.5 and 17.7 kg ha^{-1} in the mature and the young pine stand, respectively, in 1998. These values are similar to the values (19.6–24.6 kg ha^{-1}) obtained by Lee *et al*. (1996b) from two 25-year-old jack pine (*P. banksiana*) stands in Manitoba, Canada. However, they are higher than the total tree pollen values, approximately 7.7–9.0 kg ha^{-1}, from a pine–spruce–poplar mixed forest in Manitoba, Canada. The values are also greater than the 0.9–3.0 kg ha^{-1} range reported for Jeffrey pine stands in Nevada (Stark 1973), but fall within the very broad 3.5–80.0 kg ha^{-1} range estimated for inside and outside white pine and red pine (*Pinus strobus* L., *Pinus resinosa* Ait., respectively) stands in northern Wisconsin (Doskey & Ugoagwu 1989). However, our values are lower than the 55–96 kg ha^{-1} year^{-1} and 89–170 kg ha^{-1} year^{-1} values reported for *P. densiflora* forests in Japan (Saito & Takeoka 1985; Sekiguchi *et al*. 1986). The discrepancies in the pollen production and deposition values between Japan and Korea may arise from the amount of pollen intercepted by tree trunks and leaves in the process of deposition. This may explain why pollen production of pine forests in Japan was higher than in Korea (i.e. pollen was collected directly from the flowers in the Japanese studies). Moreover, we have to consider pollen dispersal distance and the patterns observed inside and outside forests. Buell (1947) reported that from 0.1 mile (~160 m) out there was a gradual decrease in the amount of pollen deposition with increasing distance from the source trees. Thus, 15% of the pine pollen that fell in the forest fell at 0.2 mile out and 10% fell at 0.25 mile out. We believe that considerable amounts of pine pollen are carried out from our relatively small study site (~1.2–2.5 ha). Another study using two types of gravity samplers revealed that the pollen count using an IS-Rotary sampler was greater than that using a Durham counter (Koto & Kishikawa 2001). According to the results of our preliminary examination, the pollen count decreased by 20% because of the use of an upper disk on the Durham collector compared to sampling conducted without the upper disk. Therefore, the pollen deposition values obtained in this study are conservative values.

Large quantities of pine pollen were liberated over approximately 12–14 days, with peak pollen deposition occurring on 20 April in the study area. In Manitoba, Canada, pollen anthesis lasted for 10–14 days and peak pine deposition occurred from 3 June to 12 June (Lee *et al*. 1996a). The study area is located at latitude ~36°N and Manitoba site is located at ~55°N. Therefore, there is approximately 19° difference in latitude between the Taegu and Manitoba sites and this difference results in a 48-day delay in pine anthesis. Annual variations in the amount and duration of pollen production were reported in several studies (Saito *et al*. 1991; Lee *et al*. 1996b). Saito and Takeoka (1985) found that pollen production rates ranged from 55 to 96 kg ha^{-1} year^{-1} in a 35-year-old *P. densiflora* forest during 1979–1983. Sekiguchi *et al*. (1986) also reported that annual pollen production in 1983 (170 kg ha^{-1} year^{-1}) was approxi-

mately double that of 1982 (89 kg ha^{-1} $year^{-1}$) in an 85-year-old *P. densiflora* forest.

Pollen macronutrient concentrations are similar between *P. densiflora* and *P. rigida*. In general, total macronutrient levels in *P. densiflora* and *P. rigida* are similar to pollen from other pine species (e.g. *P. banksiana* in Canada). *Pinus banksiana* pollen collected from Manitoba, Canada had a lower sulfur concentration than other pine pollens from South Korea. These differences may result from the soil properties in which the pine trees grow; however, further studies are required.

Species with low nutrient requirements, such as *P. banksiana*, have been shown to maintain acceptable growth rates on sites of low fertility (Morrison 1973). *Pinus densiflora* is one species that has such characteristics and so must be able to grow at a certain rate at low fertility sites. At one pine forest stand in Korea, *P. rigida* trees annually delivered 3157 kg of litterfall and this was equivalent to N 16.4, P 0.4 and K 2.1 (kg^{-1} ha^{-1} $year^{-1}$) (Chang & Ko 1982). Total macronutrient inputs by precipitation in a *P. densiflora* stand in Korea are N 13.1 kg ha^{-1}, K 14.1 kg ha^{-1} and Mg 19.2 kg ha^{-1} (Kim 1994). Corresponding values for nutrient deposition by pollen (at the mature pine stand; 27.5 kg ha^{-1} $year^{-1}$) are N 0.55 kg ha^{-1}, P 0.08 kg ha^{-1} and K 0.24 kg ha^{-1}, suggesting that pollen contributes relatively little to the overall stand nutrient dynamics. It must be recognized, however, that pollen deposition occurs over a brief, 2-week period in mid to late April. A previous study showed that the majority of water-extractable pine pollen macronutrients were solubilized within 24 h in water (Lee *et al*. 1996b). In addition, pollen grains are broken down within 2 months (Stark 1972), suggesting that pollen may be an important source of macronutrients during the critical early growing period. In a study of *P. densiflora* canopy through fall and stem flow, Kim (1994) noted 'increasing of large quantities of macronutrients from May to August samples…' and excluded it from further analysis. In his study, the amount of Mg reached a peak in samples collected in June and July at 5.5 kg ha^{-1} and 4.7 kg ha^{-1} levels, respectively. It is also possible that the high early summer K through fall levels reported by Foster and Gessel (1972) are attributable to pollen contamination.

Macronutrient deposition by pine pollen is concentrated temporally in spring. Pollen deposition is highly episodic, and nutrient concentrations and deposition rates of pollen grains are high (Stark 1973). In contrast, decomposition rates of pine litter are much lower, resulting in the accumulation of considerable amounts of litter over time (Foster & Morrison 1976; Prescott *et al*. 1989). Although the annual contribution of nutrient mass by pollen is small compared to that of litterfall (Stark 1972; Foster & Morrison 1976), the rapid turnover rate of pollen nutrients combined with episodic deposition suggests that pollen may play a disproportionate role in temperate pine forest nutrient cycling. Stark's (1972) study revealed that most of the elements delivered in the pollen cells are mobilized within 2 months, whereas it takes ≥5 years for the total release of the elements contained in needle fall alone.

As early as the 1930s, Bransvheidt (1930) revealed the nutritional and stimulatory value of pollen to fungal growth. Stark (1972, 1973) reports that pine pollen enhances decomposition by providing an early summer macronutrient pulse to decomposers in the litter fermentation layer. He also reports that after spring pollen rain, the fermentation layer increases in N and P. Nutrients from pollen that is added to the temperate pine forest floor are not likely to be significant to tree growth directly (Stark 1972). In Stark's (1972) study, the total potential elemental input of litter ha^{-1} $year^{-1}$ is 615-fold that of the potential elemental input from pollen rain ha^{-1} $year^{-1}$ (for the 10 elements examined). However, in his study, pollen deposition was only 0.9–3.0 kg ha^{-1} $year^{-1}$ in a Jeffrey pine stand. The value recorded in our study (17.7–27.5 kg ha^{-1} $year^{-1}$) is approximately 1/115–180-fold that of *P. rigida* litterfall in Korea. If we take pollen nutrients into account, the contribution rate of pollen in the annual nutrient input is much higher in our study (N 1/30, P 1/5, K 1/9 that of litterfall). In a 30-year-old *P. banksiana* stand, tree litterfall delivered N 20.5, P 1.2, K 4.9 (kg ha^{-1} $year^{-1}$) and pine pollen deposition in 25- year-old *P. banksiana* was N 0.49, P 0.07, K 0.20 (Foster & Morrison 1976; Lee *et al*. 1996b). This shows that pollen rain delivers approximately 1/17–1/42 of the annual nutrient input by litterfall in jack pine stands.

Hutchison and Barron (1997) found that many lignicolous fungi are capable of degrading pollen. In Korea, pine mushrooms (*Tricholoma matsutake* Sing) are one of the most important edible mushrooms in pine forests. Fruit bodies of pine mushrooms appear from early August to the middle of October and the production of pine mushrooms begins in 15–30-year-old pine trees and reaches maximum production in 40–60-year-old pine trees. Lee (2000) reported that pollen-treatment fungal growth experiments suggest that pine pollen nutrients are very important for ectomycorrhizal fungal growth. Therefore, macronutrient deposition by pine pollen is concentrated temporally and, in combination with warm temperatures, can be an important seasonal nutrient source for ectomycorrhizal growth in temperate and boreal forests. Further studies should focus on understanding the function of pine pollen rain in terrestrial ecosystems.

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