Pollen's contributions to Siberias forests

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Abstract

How pollen shapes forests and forestry can be illustrated using Siberia's boreal forests which have historically produced some of the highest pollen concentrations in the Northern Hemisphere. Pollen's contributions are categorized as follows: 1) forests and timber, 2) nontimber products and services and 3) emerging research at the forest-atmosphere interface. Examples are drawn from *Pinus sylvestris* (Scots pine), *Pinus sibirica* (Siberian stone pine) and *Pinus koreansis* (Korean pine). Pine pollen is not only vital to timber and nontimber products but it serves as a well-studied model system for atmospheric studies.

Keywords

Boreal forests; Diplohaplontic life cycle; *Pinus* spp.; Long-distance dispersal; Long-range transport; Bioaerosols; Atmospheric biology; Aerobiology

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"…a higher plant is at the mercy of its pollen grains." J.B.S. Haldane (1932)

1 Introduction

Pollen has a hidden yet essential role for forests, timber and nontimber production. This is illustrated using Siberia's vast forested expanse (Figure 1) which is 78% of Russia (Kukavskaya et al. 2013; Box 1). Here too we introduce forest pollen's emerging role in atmospheric research.

Box 1. Reforesting Siberia.

Siberia's forests are shrinking. Over one million hectares of logged sites are bare ground, classified as "non-recovered" because there has been no natural regeneration. Forest losses can be traced to several causes. First, non-recovered areas carry a high fuel load and are thus more fire-prone than forests (Kukavskaya et al. 2013). Another cause is exotic pests and pathogens introduced by global trade (i.e. Semizer-Cuming et al. 2018). A third cause is intensive logging, often illegal. Illegal logging accounts for 15 to 20% of timber harvest in Russia (Gauthier et al. 2007). Since 2007, timber lost to illegal logging has more than doubled in four years in Russia's eastern Siberia, also known as the Far East. Illegal logging now accounts for 50 to 70% total timber volume, up from 22,000 m^3 in 2007 to 58,000 m^3 in 2010 (Kukavskaya et al. 2013). A fourth cause is increased wildfire risk on melting permafrost (Tchebakova et al. 2016). All point to a need for Siberia's reforestation.

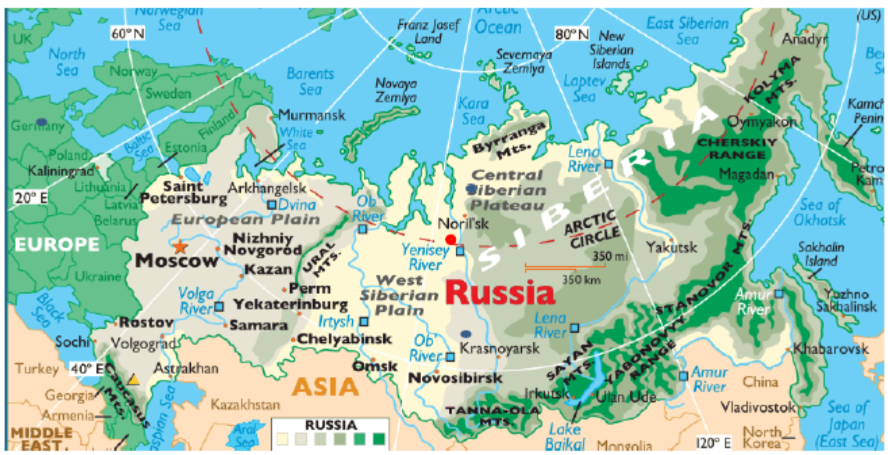

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Figure 1. Siberia's forested areas are vast. Central Siberia is defined by the north-flowing Yenesei River which ends at the Igarka port on the Arctic Sea. The Yensei River runs through Krasnoyarsk krai, starting south of its largest city, Krasnoyarsk. The Yenesei River joins its headwater tributary Angara River near the historic city of Yeniseysk. East of that juncture, the Angara River connects to the Ilim River. Siberia's most intensive logging has been in these three river basins. Pine pollen concentration reports come from Novosibirsk, Lake Baikal and Finland, the ZOTTO tall tower observatory is 600 km due north of Krasnoyarsk and the Amur River's *Pinus koreansis* forests produce edible pine seeds preferred by Amur tiger's prey.

Reforestation requires pollen management. If relying on natural regeneration then large-scale pollen production is needed to produce large seed quantities (Figure 2). Likewise, if relying on planted seedlings then pollen is required for sound seed collected for forest nurseries which supply seedlings. This is also true for those who rely on seed orchards. Seed orchards rely on high pollen quality as well as sufficient pollen quantity. Pollen quality improves with careful collection, processing, storage and application techniques. This is particularly true for advanced-generation seed orchards where selections come from tree breeding programs rather than wild-tree selections. Each breeding cycle advances using selective breeding and testing to advance genetic gain. Pollen quality becomes more important with selections from each new breeding cycle. All forms of reforestation in Siberia thus depend on live pollen.

Three species are discussed here as examples: *Pinus sylvestris* L. (Scots pine), *Pinus sibirica* Du Tour (Siberian stone pine) and *Pinus koraiensis* Siebold & Zucc. (Korean pine). *Pinus sylvestris*, a hard pine, is the major timber species for Siberia and elsewhere in Europe, Eurasia and Turkey while the other two are soft pine species valued for edible pine conelets and seeds. Species-level identification is rarely possible for the third role, using pine pollen as a model system for research at the forest-atmosphere interface. Foresters and researchers in Siberia and other higher-latitude forests might benefit by knowing more about pine pollen as a well-studied model system connected to atmospheric sciences and human health. In contrast to the live pollen necessary for timber and nontimber products, pine pollen is hypothesized to affect atmospheric events whether it is alive or dead, intact or ruptured. Understanding the full importance of pollen's Siberia's forests requires background about the forest tree life cycle and pollen biology basics.

Figure 2. *Pinus sylvestris* pollen strobili on a tree located north of the Yenesei River are still green, not dry enough for release.

2 The diplohaplontic life cycle

Forest trees, like other higher seed plants, have a diplohaplontic or two-phase life cycle. The dominant phase is the diploid sporophyte and the transient phase is the haploid gameophyte, male and female. The gametophyte phase is not to be confused with gametes. The gametophyte is a multicellular organism, best thought of an extra stage missing in the life cycle of humans and vertebrates. When adult trees, or sporophytes, reach reproductive competence then they begin production of specialized cells which develop into female or male gametophytes. This occurs when a reproducing pine tree develops two separate cell lineages at its branch tips, or apical meristems (heterospory). One is a female lineage and the other is a male lineage. Each type of cell lineage develops its own type of haploid gametophytes. Each gametophyte develops one or more gametes. The union of female and male gametes, or fertilization, forms the embryo which matures into a seed. The seed germinates into a seedling, a young sporophyte. The sporophyte may survive to grows into a mature tree itself. This is the diplohaplontic life cycle of all seed plants, including pines and other forest trees.

3 Pine pollen biology

A pollen grain has a two-part structure. Its outer coating, or exine, is a multilayered pollen wall supplied by the adult sporophyte. This pollen wall surrounds the immature haploid male gametophyte. The pollen wall has an aperture where the gametophyte will produce a germination tube late in its development (i.e. Williams 2009). The pollen germination tube emerges through the exine's aperture late in development, after the pollen grain has been released, transported, deposited and hydrated. The germination tube is where its gametes, or two sperm nuclei, will form later in pollen development. Pollen germination and its fertilization of the egg cell are separated by year or more (Singh 1978). This developmental sequence, from pollen formation to its germination and fertilization, is essential to understanding how Siberia's forests depend on pollen.

4 Pollen's contribution to timber

Siberia has a few forest species including some belonging to the genus *Pinus* spp. (Tchebakova et al. 2016). This low species number is remarkable given its vast forested expanse. The Russian Federation has 22% world's forested area, of which 21% is standing timber, Over three-quarters is in Siberia (Kukavskaya et al. 2013). Logging *Pinus sylvestris* in central Siberia began in the 1840s (Hellmann et al. 2015). Historically, logging is concentrated around the Arctic-flowing Yenesei River area (Figure 1). This river's headwaters start near the Mongolian border, flowing northward for a distance of over 2500 km. The Yenesei River divides flat boggy West Siberian Plain from the central Siberian Plateau then flows through permafrost regions at latitude 62˚ N before reaching the Arctic Sea. As an aside, note that few forest species survive on permafrost; *Larix dahurica* is the only tree species found on the type of permafrost which has an active layer less than two meters (Tchebakova et al. 2016). Permafrost's occurrence, its active layer and its depth are the crucial controlling factors for Siberia's forest distribution, forest growth and species composition.

Widely separated populations of *Pinus sylvestris* in Siberia and the rest of its extensive range are connected by pollen. Pine pollen concentration is heavy in Siberia relative to other forests in the Northern Hemisphere. Forests in Europe, Asia and North America ranging from 33° to 64° N latitudes release heavy forest pollen clouds from March to June (Williams and Després 2017). In a meta-analysis of 25 pollen emissions studies, eight locations had the highest pollen concentrations ($>10^4$ m^{-3}) and three of these were near or inside Siberia. Of these three, one study was in eastern Siberia at Lake Baikal (Figure 1; Matthias-Maser et al. 2000) and another study was in western Siberia at Novosibirsk (Figure 1; Golovko et al. 1999). A third study was conducted at the Hyytiälä Finland field station above latitude 61˚ N (Manninen et al. 2014). We have not yet found pine pollen concentrations for central Siberia.

5 Pollen's contribution to nontimber products

Pollen germination is necessary for pine *varenya* and edible pine seeds from Siberia (Figure 2). Pine *varenya* is made from tender first-year conelets harvested right after pollen germination inside the ovules in a female strobilus (Figure 3). If pollen grains landing on the ovules do not germinate then the female strobilus dies before reaching the closed-scale stage for jam-making.

Edible pine seeds, locally known as pine nuts or cedar nuts, also require pollen germination and successful fertilization. Without fertilization, developing ovules in the conelet die, making no filled seeds. This means that pine pollen grains must be capable of both germination and fertilization. Edible pine seeds support wildlife, especially the prey of the Amur tiger (Box 2) which lives in the forests along the Amur River forming the border between eastern Siberia and China (Figure 1).

Figure 3. Nontimber example for pollen. Pine cone *varenya* is a jam made from tender immature pine conelets harvested soon after pollen germination.

Figure 4. A pine cone statue, a cultural expression of how highly forests are valued, in Krasnoyarsk krai where 50% of Siberia's pine timber is logged.

Box 2. *Pinus koraiensis* habitat of the Amur tiger.
Russia's Far East office of WWF-Russia has raised awareness of the Amur River (Figure 1) along the Russia-China border and its Amur tiger (a subspecies of *Panthera tigris*) populations. The Amur tiger relies on prey which consume *Pinus koreansis* seeds. Accelerated illegal logging in this region has cut edible pine seed production. As a result, *Pinus koreansis* has been added to CITES Appendix III although not yet endangered according to the IUCN Red List (Thomas and Farjon 2013). Pine forests and their products in Siberia are integral to cultural identity, diet and economic well-being (Figure 4).

6 Pollen's contribution to research at the forest-atmosphere interface

Pine pollen has become a well-studied model system. Research has elucidated its cell biology, aerodynamic properties, shape, size, phenology, optical properties and genomics. Research protocols are readily available for collection, processing, storage, germination testing and dispersal (Williams 2009). Dry pine pollen can be frozen for years yet still retain its capacity for germination and fertilization when thawed. These protocols are used to track long-range transport and its vertical uplifting into the planetary boundary layer and upper troposphere (i.e. Mandrioli et al. 1984). Using pine pollen as a model system has led to its contributions within a new area of atmospheric research.

Pine pollen is a seasonal component of airborne biological particles, also known as bioaerosols. The more precise definition is primary biological aerosol particles (PBAPs) (Jaenicke et al. 2007). PBAPs are size-defined biological particles, alive or dead, which have a radius > 0.4 um. On average, PBAPs compose 5 to 50% of atmospheric aerosols (Jaenicke et al. 2007; Fröhlich et al. 2016) but this contribution rises to 65 to 80% during peak pollen release, as shown above Siberia's Lake Baikal forests (Matthias-Maser et al. 2000). This study also shows that the composition of the PBAP fraction changing with eastern Siberia's seasons.

Pine pollen's role in bioaerosols has led to new research inquiry at the forest-atmosphere interface. Pollen links higher-latitude Northern Hemisphere forests to atmospheric research. This research has been conducted in Siberia using high-altitude aircraft campaigns, satellite imagery, a tall tower observatory (Box 3) and unmanned aircraft vehicles (UAVs or drones). All methods can benefit from in-flight identification of different particle types. This and other research gaps are reviewed here. We hypothesize that pine pollen can be used as a tracer biological particle for long-range transport in the upper atmosphere.

Box 3. Tall-tower research at the forest-atmosphere interface.
ZOTTO is the tall tower research facility is maintained by the Sukachev Institute of the Forest at Siberian Federal University through a joint agreement with the Max Planck Institute of Biogeochemistry in Jena Germany (Heintzenburg et al. 2013; Mikhail et al. 2017). Surrounded by *Pinus sylvestris* forests, its coordinates are 60.8º N 89.35º E near the western banks of the Yenesei River. ZOTTO measurements determine whether boreal forests act as sink or as sources for carbon dioxide and identify origins of atmospheric aerosols, a general circulation models (GCM) for earth systems. Siberia's boreal forest carbon budget shifts sink to source depending on whether wildfire, logging or heavy industry is taking place.

7 Pine pollen dispersal and its components

Pollen has been long thought to be "too heavy, too little" to contribute the rich milieu of bioaerosols floating in the atmosphere but this is no longer the case. Huge volumes of pine pollen are released seasonally from the higher-latitude forests and it is subject to long-range transport in the upper atmosphere for days (e.g. Mandrioli et al. 1984; Lindgren et al. 1995; Williams and Després 2017). Understanding how pollen moves within the atmosphere (Figure 5) is central to following pollen's role in atmospheric research.

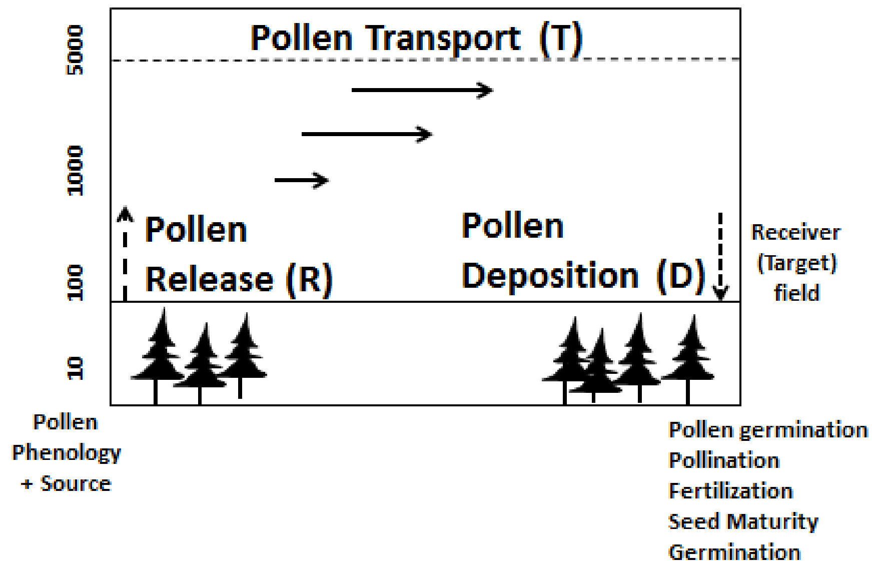

Figure 5. Pine pollen disperses across all distance scales. Dispersal consists of release (R), transport (T) and deposition (D). Transport requires updrafting above the forest canopy.

7.1 Pollen release component

Releasing pine pollen is a dynamic launching process reliant upon turbulent kinetic energy. This process is distinct from passive release which relies on gravity alone. Pine pollen sacs open after reaching a low internal water balance. The sacs dehisce, releasing pollen in a state of highly dehydrated anhydrobiosis. Moderately hygroscopic, newly released pine pollen is prone to wicking up atmospheric moisture (Greenwood 1986; Bohne et al. 2005).

The release of dehydrated pine pollen requires strong winds gusting through the forest canopy. Each gust causes the long flexible branches at the base of a tree's crown to sweep in circular arcs so that pollen-bearing branches are surrounded by yellow clouds of pollen (Jackson and Lyford 1999). A wind gust must cross a threshold wind speed of 0.5 m s^{-1} at which point the wind's airflow becomes stronger than the pollen grain's boundary layer adhesion to its microsporangial tissue. Although most pine pollen is released in daylight hours, steady amounts of *Pinus* spp. pollen is released at night (i.e. Lindgren et al. 1995; Pulkkinen and Rantio-Lahtimaki 1995; Williams 2008). A fraction of pollen is uplifted above the forest canopy by swirling eddies then the pollen is transported by strong horizontal winds at speeds of 50 km/h or more (Katul et al. 2006). Still more pollen is updrafted into higher altitudes at the planetary boundary layer (i.e. Mandrioli et al. 1984).

Pine pollen is prone to vertical updrafting because it is more spore-like than seed-like. Adapting seed dispersal models for predicting pollen dispersal distances are too conservative (i.e. Kuparinen et al. 2009). *Pinus taeda* pollen has aerodynamic prpoerties more akin to lichen soredia, club moss spores and smut fungi spores (Williams 2017).

7.2 Pollen transport component

How a pollen grain interacts with atmospheric processes during its transport is a function of its taxon-specific properties. We cannot generalize about all pollen types or all types of forest pollen. For example, insect-dispersed angiosperm pollen tends to cluster and these clusters alter aerodynamic properties. Other pollen types rupture into fragments or subpollen particles (Rogers and Levetin 1998; Pummer et al. 2012; Augustin et al. 2013; Dreimeier et al. 2016). So far, pine pollen is thought stays intact after hydration (Williams 2013; Hader et al. 2014) but other studies do not concur (i.e. Steiner et al. 2015).

Shape allows for easy identification of pine pollen grains (Williams 2009). Most pine pollen has a two-eared shape due its two air-filled sacs, or sacci, on either side of the aperture. Sacci influence its terminal or settling velocity (V_t) value which is estimated to be as low as 2.1 to 2.3 cm s^{-1} (Williams 2008; Niklas 1984). This means that pine pollen is far more buoyant than maize pollen (Williams 2008) even after accounting for its smaller size (~ 50 μm vs. 76 μm). Pine pollen has another remarkable property: unlike maize pollen, it mostly retains its shape and size during transport because its exine is thick and wettable (Bohne et al. 2003, 2005).

Pine pollen grains get updrafted by convective currents rising from the earth's surface. Updrafting also occurs by thermal inversions or strong cumulus cloud updrafting during thunderstorm formation. Pollen grains ascend into the atmosphere within air parcels and as single grains in a well-mixed condition in the atmosphere (Womack et al. 2010). A variety of atmospheric mechanisms can updraft pollen into the atmosphere.

Pine pollen is thought to often concentrate with other atmospheric lifeforms in the expanding planetary boundary layer (PBL) during daylight hours then descend as the PBL contracts at night as convective heat from the earth's surface dissipates (i.e. Williams 2020). While aloft, a pollen grain is subject to many atmospheric processes with other particle types. Depending on the process, a pollen grain can be transported by winds or water, captured by ice or merely fall back to the earth's surface with gravity (Figure 1). At higher altitudes, a few pollen or subpollen particles mingle with other biological particles and mix with dust, soot, pollutants and solutes. All shape its chances of capture inside mixed-phase cloud layers where supercooled water and ice coexist at freezing temperatures (0 to -36^{o} C). How cloud glaciation processes interact with biological particles, or bioaerosols including pollen is a wild card in accurate climate forecasting (Boucher et al. 2013).

Pine pollen has a well-documented history of long-range transport. Found at sea at distances of 1000 km from land, pine pollen has been recovered at a distance over 3000 km from source above the Arctic treeline (i.e. Campbell et al. 1999; Rousseau et al. 2006). Pine pollen has been deposited by raindrops (Busse 1926), having been found in snow and hailstones too.

Few studies have measured pollen concentrations at higher altitudes. One aircraft study reported by Rempe (1937) asserted that 40% of the pollen concentrations at ground level were present at altitudes of 2000 m above the Leine Valley in north-central Germany. Later aircraft studies also show that low concentrations of pollen gradients are found at altitudes from > 5000 m above Wyoming USA (i.e. Mandrioli et al. 1984). The pollen gradient question is being could be resolved with better sampling methods. Atmospheric sampling could be more efficient with automation of in-flight optical identification of pollen types and other biological particles.

7.3 Pollen deposition component

Deposition can be influenced by the rise and fall of the planetary boundary layer, by precipitation scavenging or simply gravitational settling. Pollen deposition, or the process of pollen returning to the earth's surface, is often reported as a blanketing phenomenon (Williams 2020). Historically, pine pollen blanketing has been so extreme that piles of pollen can be swept from rooftops (Lindgren et al. 1995). Public health accounts are also on record (Wilson 1879). A medical doctor wrote a letter to *Nature* resolving that a blanketing of yellow dust over a Great Britain village was caused by pine pollen, not hellish sulfur powder. Atmospheric factors determining massive pollen deposition from higher-latitude forests in the Northern Hemisphere are poorly understood (Williams 2020).

8 Research gaps at the forest-atmosphere interface

Given that pine pollen is robust, intact, smaller, easily identified and produced in plentiful quantities (Williams and Després 2017), it may have experimental use as a coarse bioaerosol tracer. Even so, bacteria and fungal spores do ascend higher and longer due to smaller size and year-long ubiquity.

8.1 Research Gap 1: Pollen's interaction with cloud ice

Pollen lofted into the upper atmosphere may be captured by winds, water or ice. The capture process is studied at a particle level mostly in lab simulation studies for benefit of atmospheric research. Pollen can serve as cloud condensation nuclei (CCN) and thus influence cloud microphysical properties (Murray et al. 2012). Any biological particle in the upper atmosphere is capable of forming CCN if the particle's surfaces are wettable (Després et al. 2012; Froelich et al. 2016). How active pollen and other aerosol particles are as cloud condensation nuclei (CCN) depends on their hygroscopicity. Birch, pine and spruce pollen are all wettable and thus have the capacity to form CCN (Steiner et al. 2015) although of these, birch pollen seems most prone to rupture. We have observed that birch pollen does not rupture during rainfall.

Another cloud glaciation process, ice nucleation (IN), is exceedingly rare and thus difficulty to measure. Ice nucleation is hypothesized to occur at warmer temperatures when particles, biotic or abiotic, are present than if they are absent. Biological particles are thought to trigger ice nucleation whether alive or dead, intact or fragmented and this is part of bioprecipitation. This is a difficult hypothesis to test because what happens in clouds is so difficult to study experimentally. Presumably, ice nuclei are jostled by atmospheric turbulence so that they collide. Upon collision they grow, or accrete into frozen cloud droplets during horizontal transport. Ice nucleation and subsequent cloud formation take days during which ice-nucleated particles are carried far from source. Once heavy enough, frozen drops descend as precipitation.

These will number among the water-insoluble particles inside frozen or thawing precipitation.

Atmospheric verification has not been reported using aircraft for forest pollen either in ice nucleation and ice crystal residues. Laboratory experiments simulate atmosphere conditions (i.e. Diehl et al. 2002; Augustin et al. 2013; Hader et al. 2014; Steiner et al. 2015; Dreischmeier et al. 2016). Immersion freezing accounts for 85% of ice nuclei events; pine pollen forms ice nuclei in the immersion freezing mode (Diehl et al. 2002). Ice nuclei form on *Pinus sylvestris* pollen at below-freezing temperatures of -4° to -8°C. By -20°C, 100% of pine pollen grains have ice nuclei (Diehl et al. 2002). How this process happens in the upper atmosphere is not known.

8.2 Research Gap 2: Climate change effect on pollen transport distances

Pine pollen has been a model system for climate sciences so far. Older trees do produce more pollen but whether they will produce larger quantities is not yet certain. What is clear now is that stronger wind speeds accompanying climate change will transport pine pollen longer distances from source (Kuparinen et al. 2009). Another related question is whether pollen germination and fertilization will also be affected by climate change.

8.3 Research Gap 3: Optical identification of pollen during transport

Optical identification seems feasible given that each bioparticle, pine pollen included, has a unique spectral signature. These spectral properties were first observed in nature when ambient pollen concentrations are so high that rainbow-like pollen coronas formed. Pollen coronas form during clear skies in daylight hours in late spring and early summer when pollen concentrations exceed 10^2 to 10^3 m^{-3} at canopy level (i.e. Parvainen et al 1994). Oddly, corona shape is also thought to correspond to the shape of pollen suspended in the atmosphere (Parvainen et al 1994). Pollen corona are viewed as visual proof of species-specific optical properties.

Similarly, birch, pine, spruce and other forest pollen have been identified in Alaska USA at altitudes up to 2 to 3 km above ground level using a ruby LIDAR (Sassen 2008). These LIDAR readings were taken when birch pollen concentrations reached 1153 grains m^{-3} on May 14 2008. Similar findings were reported in South Korea where investigators used a green-light LIDAR (532 nm) to detect rising pollen clouds up to 2-km altitudes between 1200-1400h daily. Canopy-level forest pollen concentrations were between 10^2 to 10^3 grains m^{-3} (Noh et al. 2013). They noted that pollen concentrations detected by LIDAR are composed of pollen from several forest species. To sort this, the spectral signature of each forest pollen type would have to be calibrated using laboratory studies (e.g. Pölker et al. 2013). Whether this can be done via high-altitude aircraft sampling as reported by DeLeon-Rodriguez et al. (2013) is yet to be seen.

9 Conclusions

Pollen has a hidden role in sustaining Siberia's forests. Heavy pollen concentrations are a necessity for large seed and cone harvests, whether reforestation depends on natural regeneration or planting. Similarly, edible pine seeds and pine varenya production depend on live pollen. For forest-atmosphere research, pine pollen has potential to exert effects whether alive or dead.

Here we provide support for two assertions. First, pollen is vital to Siberia's forests, its forest products and global atmospheric research. Second, our working hypothesis is that pine pollen might serves as a model tracer system for coarse biological particles given its aerodynamics properties, its observed transport via wind and precipitation across a range of distance scales and its potential interaction with atmospheric processes. It is true, as Haldane wrote, that forests are truly at the mercy of pollen but Siberia's forests tell us something more: that pollen grains influence forests no matter whether they are dead or alive.

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