OPTICS OF CLUSTERS, AEROSOLS, AND HYDROSOLES

# Generation of Secondary Organic Aerosols on Needle Surfaces and Their Entry into the Winter Forest Canopy under Radiometric Photophoresis

M. P. Tentyukov<sup>a, b, \*</sup>, B. D. Belan<sup>a, \*\*</sup>, D. V. Simonenkov<sup>a, \*\*\*</sup>, and V. I. Mikhailov<sup>c, \*\*\*\*</sup>

<sup>a</sup> V.E. Zuev Institute of Atmospheric Optics, Siberian Branch, Russian Academy of Sciences, Tomsk, 634055 Russia <sup>b</sup> Pitirim Sorokin Syktyvkar State University, Syktyvkar, 167001 Russia

<sup>c</sup> Institute of Chemistry, Komi Scientific Center, Urals Branch, Russian Academy of Sciences, Syktyvkar, 167000 Russia

\*e-mail: tentukov@yandex.ru \*\*e-mail: bbd@iao.ru \*\*\*e-mail: simon@iao.ru \*\*\*\*e-mail: system14@rambler.ru Received January 19, 2022; revised March 5, 2022; accepted April 1, 2022

Abstract—We analyze the results of the laser granulometry of a nanosized fraction of settled aerosol substance and UV spectrometry of water washouts from the surfaces of different-age needles of four forest-forming plant species. The activity of efflorescence of phenolic compounds onto different—age needle surfaces is estimated for the period of winter dormancy of plants. A possibility is shown for the secondary organic aerosol production as a result of photoactivated reactions between phenolic compounds and deposited aerosol substance. It is discussed how secondary organic aerosols can enter the winter forest canopy under the influence of the radiometric photophoresis. The secondary aerosol photophoresis in the field of IR radiation, leaving the snow cover surface ("snow" photophoresis), is speculated to affect significantly the vertical transport of the secondary organic aerosols in the winter coniferous forest canopy.

**Keywords:** dynamic light scattering, UV spectrometry, efflorescence, polyphenols, secondary organic aerosols, radiometric photophoresis, needles, winter

DOI: 10.1134/S1024856022050219

## INTRODUCTION

The authors of work [1] presented the results of laser granulometry and UV spectra of water washouts from different-age needles, based on which the assumed that phenolic species can serve as precursors for organic aerosols. It should be noted that phenolic species are ubiquitous in the plant world [2-4]. At present, natural compounds are found to include some hundreds of thousands of phenolic species [5-7]and, in particular, tens of thousands of flavonoid structures in plants [8]. Phenolic compounds are synthesized as monomers, oligomers, and polymers and are encountered in almost all plant cells [9]. Under normal conditions, most of the ordinary phenols are colorless acicular crystals rapidly darkening in air. They are characterized by relatively narrow temperature range of melting and evaporation. For instance, the melting temperatures are  $\sim 100^{\circ}$ C for flavone and  $316^{\circ}C$  for quercetin [2, 3].

Phenolic compounds are weakly soluble in water and very soluble in organic solvents. Their prominent feature is the high reaction capacity because the molecule of ordinary phenol is a polar compound consisting of a benzol core and hydroxyl group. Polyphenols may react with metals to form chelate compounds, bind with organic acids, amines, and alkaloids; they are characterized by hydroxylation, methylation, glycosylation, acylation, methoxylation, and condensation reactions. It is also important that phenolic compounds have characteristic absorption spectra in specific UV regions [10], allowing them to inhibit the origination of active oxygen species in plant cells [11, 12]. Photo inhibition of singlet oxygen by polyphenols and, in particular, flavonoids, reduces the UV absorption by plants in the wavelength range 280–315 nm [13] and protects plant from photooxidative stress, which is important for the life of coniferous plants during winter.

Needles remain green because metabolic processes in coniferous plants continue in winter [14]. Under the conditions when photosynthesis is halted due to low temperatures [15], but the needle chloroplasts continue functioning [16, 17], polyphenols become much more important in protecting green leaves of coniferous plants from photooxidative damage [18, 19], suggesting that the production of the secondary organic aerosols associated with entry of polyphenols onto needle surfaces during efflorescence persists into winter. Therefore, the purpose of this work is to elucidate the specific features of production of the secondary organic aerosols during efflorescence of polyphenols onto the surfaces of different-age needles and to identify how polyphenols enter the forest canopy during the winter dormancy of plants.

## TARGET STRUCTURES AND METHODS

Needle samples were collected in late December 2021, in the period of the winter dormancy of plants. The experimental site was on the territory of Botanic Garden of Pitirim Sorokin Syktyvkar State University, 4 km west of Syktyvkar in the suburban green zone. To collect needle samples in different age fractions, we chosen four model tree species in groups of two: 18-25-year-old Siberian pine (Pinus sibirica Rupr Maur Tour) and Scotch pine (Pinus sylvestris L.) and 10-yearold undergrowth of European fir (Abies alba Mill.) 30–40-year-old Siberian spruce (*Picea obovata* Lebed.). The needles in age fractions were sampled from the second-order branches in the lower third of the crown in each tree species within eastern bearings (in azimuthal sector between 45 and 135°). The fractional composition of the deposited aerosol substance in samples of different-age needles was studied by the method of dynamic light scattering.

Dynamic light scattering method. The method essentially consists of recording the time fluctuations in the intensity of the laser beam scattered in a disperse medium. When the laser beam passes through local particle concentrations, partial scattering of light and the associated local changes in optical density of the disperse medium occur, as well as the ensuing changes in the refractive indices of light. The numerical parameters of light scattering depend on particle size, particle diffusion intensity, and viscosity of the liquid [20]. The method of dynamic light scattering is among nondestructive ones. It needs no precalibration and is equally efficient both for low particle concentrations and in the presence of particle aggregates. The measured particle size ranges from 0.5 nm to few microns. The method is characterized by the low cost of the measurements, small error, and rapidity.

Preparation of washouts from needles for granulometric analysis and UV spectroscopy. We placed needle specimens, 30 pieces in each age fraction, in glass beakers and added deionized water (50 mL). Then, the glasses were placed into an ultrasonic bath Sapfir UZV-5.7 (working frequency 35 kHz and generator power 150 W), in which the specimens were exposed to ultrasound for 5 min. A ZetaSizer Nano ZS laser analyzer (Malvern Panalytical, Great Britain) was used to determine nanoparticle sizes in specimens. Particles in the size range 1–10000 nm were measured. In each measurement of the volume particle content, the optimal accumulation time of the correlation function was automatically determined by software of the instrument; then, they were averaged. The volume content of the nanoparticle fractions in specimens was integrally calculated from the ratio (%) of the areas of the figures circumscribing these particle size distributions in linear coordinates. A Solar PB2201 (Spectroscopy, Optics, and Lasers—Advanced Developments Ltd., Belarus) spectrophotometer was used for UV spectroscopy of water washouts from needles.

### RESULTS

Frequency distribution of particles in aerosol substance over sizes in water washouts from leaf surfaces of shortleaf plants (Siberian pine and European fir) in winter needle specimens is presented as distribution histograms (Figs. 1a and 1b).

Comparison of granulometric compositions of aerosol substance with respect to six age fractions in winter samples of Siberian pine showed (Fig. 1a, 1-6) that the particle sizes (diameters *D*) lie in the range from 40–170 to 3000–7000 nm. The particle distribution is trimodal with a large variance. Large particles with diameters 3000–7000 nm are predominant (67%). Small (40–170 nm) and medium-size (170–3000 nm) particles make 2–3% and 12–48% respectively.

Specimens for European fir needles show somewhat different results. For instance, particles in six age fractions vary in size from 50 to 1800 nm (Fig. 1b, I-6), with a predominant contribution (67–81%) from large particles 3000–7000 nm in diameter. Small (75–300 nm) and medium-size (300–3000 nm) particles amke 1–5% and 17–40%. As in the first case, the particle distribution is trimodal with a large variance.

Frequency distribution of particles of aerosol substance over sizes in water washouts from leaf surfaces for longleaf plants (Siberian pine and Scotch pine) in winter needle specimens is also presented in Figs. 1c and 1d. For the Siberian pine specimens, the particles in six age fractions vary in diameter from 50 to 7000 nm (Figs. 1c, 1-6). Large particles with diameters 3000– 7000 nm are predominant (50–78%). Small (50– 150 nm) and medium-size (250–1000 nm) particles make 2–10% and 20– 44%, respectively. The particle distribution is trimodal with a large variance.

For specimens of needles of Scotch pine, the particles in four age fractions vary in size in the same limits (50-7000 nm) (Figs. 1d, I-4), again large particles with diameters 3000-7000 nm being predominant (62-74%). It is noteworthy that small (50-200 nm) and medium-size (250-1800 nm) particles make 6-7% and 18-32%. However, it should be noted that Scotch pine shows much wider size ranges of medium-size and small particles than Siberian pine does. The particle distribution is trimodal with a large variance.



**Fig. 1.** Granulometric composition of aerosol substance in water washouts from different-age needles (*1–6* indicate the needle age in years): (a) Siberian spruce (*Picea obovata* Lebed.); (b) European fir (*Abies alba* Mill.); (c) Siberian pine (*Pinus sibirica* Du Tour); and (d) Scotch pine (*Pinus sylvestris* L.)



**Fig. 2.** UV absorption spectra of water washouts from needles in age fractions from winter specimens for: (a) European fir; (b) Siberian spruce; (c) Siberian pine; and (d) Scotch pine; here, 1-6 indicate needle age in years.

Thus, a common feature for all winter specimens of needles is that the granulometric composition of different-age needle fractions is characterized by a trimodal distribution of nanoparticles with a large variance. Large particles (3000-7000 nm in diameter) are predominant, with their contribution reaching 50–74%. Small (50-300 nm) and medium-size (300-3000 nm) particles make 2-10% and 20-50%.

Content of phenolic compounds in water washouts from winter needles. Figure 2 presents results from UV spectroscopy of water washouts from different-age needles. It can be clearly seen that the water washouts for all specimens quite strongly absorb the radiation in the UV region 250–400 nm, with absorption intensity gradually decaying in the longer wavelength region.

A common feature for all specimens is a peak in the absorption zone at 275 nm, indicating that specimens of washouts comprise polyphenols, entering needle composition. At the same time, the behaviors of spectral curves somewhat differ among coniferous tree species. For instance, as compared to shortleaf species (Figs. 2c-2d), longleaf species (Figs. 2a and 2b) show UV spectra of polyphenols shifted somewhat to the longer wavelength region. Possibly, this difference in the patterns of the curves stems from the difference in the composition of phenolic compounds, which strongly vary in the content in the period of winter dormancy of plants (Table 1). Data for compiling the table, which characterizes the time series of relative variations in the content of polyphenols in water washouts from different-age needles, were extracted from the plots (Figs. 2a-2d). After comparison of these time series we can note two features. Siberian spruce shows an inversion in the content of polyphenols: the signal of polyphenol content is much stronger in water washouts from the first-year than sixth-year needles (Table 1). Moreover, the character of polyphenol accumulation on the needle surface shows no well-

Tree species	Period of winter dormancy, years
European fir	1 < 3 < 2 < 6 < 5 < 4
Siberian spruce	6 < 5 < 3 < 2 < 4 < 1
Siberian pine	4 < 3 < 2 < 6 < 1 < 5
Scotch pine	2 < 3 < 1 < 4

 Table 1. Relative variations in the content of phenolic compounds in water washouts from different-age needles in time series (according to UV spectroscopy data)

defined increasing trend of polyphenol content with aging of needles.

## DISCUSSION

As applied to higher plants, polyphenols are predominantly localized in tegmens, i.e., cuticle, epidermis, and its derivatives (hairs and trichomes) [21-24]. It is noteworthy that phenolic compounds are mainly accumulated in cell walls within tegmens, as exposed most strongly to unfavorable factors [25, 26]. Different plants are thought to have become able to synthesize phenolic compounds during their evolution, which raised their resistance to permanently changing environmental conditions [8].

Increase of polyphenol content in plant tissues and their efflorescence onto needle surface during winter plant dormancy. Comparison of quantitative parameters that determine the granulometric composition of aerosol substance in water washouts from differentage needles showed that the summer specimens are characterized by bimodal distribution of particles with diameters from 50 to 2000 nm, with small particles being predominant and making 91–96% [1]. The winter specimens are characterized by trimodal distribution, the particle diameters are 60–7000 nm; large particles (3000–7000 nm) are predominant, their percentage attains 50–74%.

CO<sub>2</sub> assimilation and the associated phloem carbohydrate transport cease in winter in coniferous plants, stomatal transpiration reduces, and the intracellular CO<sub>2</sub> concentration decreases. Therefore, for coniferous plants, keeping needles green in the period of winter dormancy, there appears a danger of photodestruction of pigment complexes and chloroplast membranes in needles [27]. It is obvious to speculate that redundant under-used solar energy also leads to the growing intracellular content of phenolic compounds, as polyphenols have sensibilization properties and, as such, favor rapid reduction of the concentration of active forms of oxygen and prevent oxidation stress [13]. It is also noted that the excessive UV radiation increases antioxidant activity and the general polyphenol (flavonoid, phenylpropanoid, and phenolic acids) content in plants [28]. Therefore, the revealed winter increase in the content of phenolic compounds in water washouts from different-age needles can be considered as a protection from photooxidative stress caused by the excessive UV radiation.

Diffusiophoresis and efflorescence of polyphenols onto the surfaces of different-age needles: generation of secondary organic aerosols. Our studies show that, during winter, coniferous trees have to partially scatter the energy of absorbed quanta of light in the form of heat in order to avoid damaging the pigment complexes and chloroplast membranes by solar radiation, the intensity of which overwhelms the capabilities of electron transport [19, 29, 30]. As a result, an ordered motion of colloid particles of polyphenols occurs in cellular parenchyma of needles and in the cells of external protective tissues due to the action of forces of molecular origin, namely, thermophoresis and diffusiophoresis [31, 32]. Ultimately, phenolic compounds may accumulate in the cells of parenchyma and external protective tissues and their excessive amount may diffuse through cellular walls of epidermis and cuticle and, through efflorescence, accumulate on the needle surfaces. Exposed to UV radiation, and with the participation of deposited aerosol substance, phenolic compounds experience photochemical conversions on needle surfaces. This process is accompanied by the generation of secondary organic aerosols, in which polyphenols are fixed according to the absorption of UV radiation in the wavelength range 250-400 nm (see Figs. 2a-2d).

Activation of secondary aerosols in the boundary layer and their entry into winter forest canopy stem from the action of radiometric forces, i.e., photophoresis. The phenomenon of photophoresis was first established by Ehrenhaft [33]. In his experiment (1917), Ehrenhaft identified an effect, during which certain air-suspended dust particles in the ray from a powerful lamp moved in the direction toward the source of radiation. The effect discovered was called photophoresis. Further studies of particle motion in the field of optical radiation showed that, because of the inhomogeneous structure and optical properties of the material composing a particle, the incident optical radiation is nonuniformly distributed over the particle volume. Therefore, either the illuminated or shaded part of the particle can turn out to be more heated. As a consequence, positive and negative photophoresis effects are distinguished [34, 35]. Studies of the particle motion in the field of optical radiation had long been just of scientific interest because no practical applications existed for this effect. In this regard, we can mention the studies of the effect of responses of evaporating aerosols exposed to solar radiation [36], as well as studies of how solar radiation influences the aerosol deposition rate in the atmosphere [37]. Interest in photophoresis showed up only with the advent of new experimental instrumentation based on the use of lasers [20, 38–40]. The possibility of tuning the wavelength of laser radiation taking into account the absorption by a specific particle substance makes it possible to discriminate them from aerosol flow, to ensure capturing and holding particles in laser beam, to carry out their separation in a liquid, and to implement optical particle levitation in air and vacuum [41-46].

Separation of secondary aerosols in the boundary layer and their entry into winter forest canopy. It was shown [1] that how secondary aerosols enter into the forest stand canopy is associated with the processes in the boundary layer. Its simplified pattern comprises separation of the laminar boundary layer from the leaf surface, with the formation of a vortical zone and a subsequent transition to turbulence.

Polyphenols and deposited aerosol substance react to give aggregates which can represent structures of alternating or interlacing inclusions of disperse particles, comprising phenolic groups. As secondary aggregates of phenolic compounds grow to a certain critical size, signified by the absence of a time trend of increasing aerosols on the surfaces of different-age needles (see Table), the energy of incident optical radiation is absorbed and nonuniformly distributed over the volume of the secondary aerosol.

The areas of temperature inhomogeneity occur on the surface and inside the aggregate of deposited aerosols and polyphenols, the optical density of which increases under UV irradiation. After colliding with the particle surfaces in the boundary layer, some air molecules are reflected from the surfaces of the heated part of the secondary aerosol with a greater speed than others reflected from colder secondary aerosol. As a result, such a particle acquires uncompensated momentum and is separated from the needle surface. Considering that the evaporation point of phenolic compounds is relatively low, we can speculate that the momentum can sometimes be amplified by the response of evaporating molecules of compounds, comprising phenolic groups. In this case, separation of larger secondary aerosols (particle size ranges from 60 to 7000 nm during winter) from needle surfaces can be expected. Further motion of the secondary aerosol is determined by the turbulence of airflows in the canopy of the forest stand and, possibly, by the action of radiometrically derived forces.

Under any conditions, and even at the lowest temperature, snow cover emits longwave radiation (intrinsic heat) and can strongly reflect solar radiation. Therefore, positive photophoresis and the associated subvertical motions of the secondary organic aerosols against the force of gravity (photophoretic levitation [44]) may occur in the field of IR radiation leaving the snow-covered surface. We suggest here that the transport of the secondary aerosols in the IR radiation leaving the snow cover be called "snow" photophoresis, to distinguish it from "solar" and "thermal" photophoresis effects [45, 46]. The snow photophoresis is thought to be a significant seasonal factor, influencing the vertical transport of secondary organic aerosols in the field of IR radiation generated above the snow cover.

## CONCLUSIONS

The method of dynamic light scattering and UV spectrometry is used to study the granulometric composition of the nanosize fraction of aerosol substance and ratios of phenolic compounds in water washouts from different-age needles in four plant species. Our results show considerably increased content of phenolic compounds and aerosol particle sizes. Our values are more than a factor of three larger than those for summer samples. Taking into consideration their capability of absorbing UV radiation, we suggest that the increased content of phenolic compounds in water washouts from different-age needles can be associated with the protection from photooxidative stress, occurring in green needles exposed to redundant underused solar energy in the period of winter plant dormancy. Some of the phenolic compounds diffuse onto the needle surfaces (efflorescence). The phenolic compounds have photosensibilization properties. equally manifested in both summer and winter, making the surfaces of winter needles the favorable sites for the photooxidative reactions between phenolic compounds and deposited aerosol substance. Therefore, the surfaces of different-age needles in the boundary layer become sites for the origination of relatively solid secondary aggregates of aerosols and polyphenols, which can be considered off-season precursors of the secondary organic aerosols in coniferous forests. During winter, they are activated in the boundary layer and enter the forest canopy in the field of IR radiation from the snow-covered surface under the effect of the positive (snow) photophoresis. Snow photophoresis can be a cause for a prolonged stay in the coniferous forest canopy of the secondary organic aerosols comprising phenolic groups. The secondary aerosols of this type have pronounced absorbing properties in the wavelength range 250-400 nm; coniferous forests occupy more than 70% of the boreal area in the Northern and Southern Hemispheres; therefore, the entry of the secondary polyphenol-containing aerosols into the surface air seems to be no less important to control, especially in winter period, than the emission of greenhouse gases.

Snow photophoresis can make a certain contribution to atmospheric radiation processes over coniferous forested massifs and, thereby, can influence the errors of remote monitoring of atmospheric pollution. The accumulation of the secondary polyphenol organic aerosols can be monitored in the near-ground atmosphere from aircraft laboratories because the nature of their migration is associated with seasonal character of the underlying surface.

### FUNDING

This study was supported by the Ministry of Science and Higher Education of the Russian Federation (V.E. Zuev Institute of Atmospheric Optics, Siberian Branch, Russian Academy of Sciences (assignment no. 121031500342-0). The theoretical analysis was supported the Russian Foundation for Basic Research (grant no. 19-05-50024) and by the Russian Foundation for Basic Research and Administration of Tomsk Region (joint grant no. 18-45-700020).

Laser granulometry and UV spectroscopy of water washouts from different-age needle fractions were accomplished within State assignment (no. 122040100040-0) at the Center for collective use Khimiya of Institute of Chemistry of the Komi Scientific Center, Urals Branch, Russian Academy of Sciences.

### CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

#### REFERENCES

- M. P. Tentyukov, V. I. Mikhailov, D. A. Timushev, D. V. Simonenkov, and B. D. Belan, "Granulometric composition of settled aerosol material and ratio of phenolic compounds in different-age needles," Atmos. Ocean. Opt. 34 (3), 222–228 (2021).
- M. N. Zaprometov, "Phenolic compounds and techniques for their study," in *Biochemical Techniques in Plant Physiology* (Moscow, 1971), p. 185–207 [in Russian].
- 3. A. Blazhei and L. Shutyi, *Plant Phenolic Compounds* (Mir, Moscow, 1977) [in Russian].
- A. Ahajji, P. N. Diouf, F. Aloui, I. Elbakali, D. Perrin, A. Merlin, and B. George, "Influence of heat treatment on antioxidant properties and colour stability of beech and spruce wood and their extractives," Wood Sci. Technol. 43 (1), 69–83 (2009).
- J. B. Harborne and C. A. Williams, "Advances in flavonoid research since 1992," Phytochemistry 55, 481– 504 (2000).
- R. A. Dixon, "Natural products and plant disease resistance," Nature 411 (6839), 843–847 (2001).
- 7. M. Carocho and I. Ferreira, "The role of phenolic compounds in the fight against cancer: A review," Anticancer Agents Med. Chem. **13** (8), 1236–1258 (2013).
- 8. V. Lattanzio, "Phenolic compounds: Introduction," in *Natural Products*, Ed. by K. Ramawat and J.M. Merillon (Springer, Berlin; Heidelberg, 2013).
- 9. M. N. Zaprometov, *Fenolic Compounds: Spread, Metabolism, and Functions in Plants* (Nauka, Moscow, 1993) [in Russian].
- M. Turunena, W. Hellerb, S. Strichb, H. Sandermannb, M.-L. Sutinenec, and Y. Norokorpic, "The effects of UV exclusion on the soluble phenolics of young Scots Pine seedlings in the subarctic," Environ. Pollut. **106** (2) 219– 228 (1999).
- G. Agati, P. Matteini, A. Goti, and M. Tattini, "Chloroplast-located flavonoids can scavenge singlet oxygen," New Phytol. **174**, 77–89 (2007).
- 12. K. M. Davies, N. W. Albert, Y. Zhou, and K. E. Schwinn, "Functions of flavonoid and betalain pigments in abiotic stress tolerance in plants," Ann. Plant Rev, No. 1, 1–41 (2018).
- 13. K. Csepregi and E. Hideg, "Phenolic compound diversity explored in the context of photo-oxidative stress protection," Phytochem. Anal. **29** (2), 129–136 (2018).

- D.A. Sabinin, *Plant Development Physiology* (Publishing House of the Academy of Sciences of USSR, Moscow, 1963) [in Russian].
- G. Oquist and N. P. A. Huner, "Photosynthesis of overwintering evergreen plants," Annu. Rev. Plant Biol. 54, 329–355 (2003).
- W. W. Adams and B. Demming-Adams, "Carotenoid composition and down regulation of photosystem II in three conifer species during the winter," Physiol. Plant. 92 (3), 451–458 (1994).
- W. W. Adams, B. Deming-Adams, A. S. Verhoeven, and D. H. Barker, "Photoinhibition during winter stress—involvement sustained xanthophylls cycle-dependent energy dissipation," Aust. J. Plant Physiol. 22, 261–276 (1995).
- B. Demmig-Adams and W. W. Adams, "Photoprotection in an ecological context: The remarkable complexity of thermal energy dissipation," New Phytol. 172, 11–21 (2006).
- 19. A. Verhoeven, "Sustained energy dissipation in winter evergreens," New Phytolgist **201**, 57–65 (2014).
- 20. B. J. Berne and R. Pecora, *Dynamic Light Scattering* (John Wiley & Sons, 1976).
- A. E. Solovchenko and M. N. Merzlyak, "Screening of visible and UV radiation as a photoprotective mechanism in plants," Russ. J. Plant Physiol. 55 (6), 719–737 (2008).
- 22. V. M. Kostina, Avtoref. of Candidate's Dissertation in Biology (IFR RAN, Moscow, 2009).
- 23. O. V. Kostina and L. E. Muravnik, "Structure and chemical content of the trichomes in two Doronicum species (Asteraceae)," Modern Phytomorph., No. 5, 167–171 (2014).
- 24. S. I. Semerdjieva, E. Sheffield, G. K. Phoenix, D. Gwynn-Jones, T. V. Callaghan, and G. N. Johnson, "Contrasting strategies for UV-B screening in sub-arctic dwarf shrubs," Plant, Cell Environ. 26, 957–964 (2003).
- 25. P. Burchard, W. Bilger, and G. Weissenbock, "Contribution of hydroxycinnamates and flavonoids to epidermal shielding of UV-A and UV-B radiation in developing rye primary leaves as assessed by ultraviolet-induced chlorophyll fluorescence measurements," Plant, Cell Environ. 23, 1373–1380 (2000).
- E. Valkama, J.-P. Salminen, J. Koricheva, and K. Pihlaja, "Changes in leaf trichomes and epicuticular flavonoids during leaf development in three birch taxa," Annal. Botany 94, 233–242 (2004).
- G. Oquist and N. P. A. Huner, "Photosynthesis of overwintering evergreen plants," Annu. Rev. Plant Biol. 54, 329–355 (2003).
- A. B. Yildirim, "Ultraviolet-B-Induced changes on phenolic compounds, antioxidant capacity and HPLC profile of *in vitro*-grown plant materials in *Echium orientale L*," Industr. Crops Products 153, 112584 (2020).
- 29. P. Bag, V. Chukhutsina, Zhang Zishan, Pau Suman, A. G. Ivanov, T. Shutova, R. Croce, A. Holzwarth, and S. Jansson, "Direct energy transfer from photosystem II to photosystem I confers winter sustainability in Scots Pine," Nat. Commun. **11**, 6388 (2020).
- 30. S. Takahashi and M. R. Badger, "Photoprotection in plants: A new light on photosystem II damage," Trends Plant Sci. **16** (1), 53–60 (2011).

- K. H. Leong, "Thermophoresis and diffusiophoresis of large aerosolparticles of different shapes," J. Aerosol Sci. 15 (4), 511–517 (1984).
- 32. B. V. Deryagin, *Theory of Stable Colloids and Thin Films* (Nauka, Moscow, 1986) [in Russian].
- 33. F. Ehrenhaft, "Die Photophorese," Ann. Phys. **361** (10), 81–132.
- 34. N.A. Fuks, *Aerosol Mechanics* (Publishing House of the Academy of Sciences of USSR, 1955) [in Russian].
- 35. O. Preining, "Photophoresis," in *Aerosol Science* (Academic Press, New York, 1966), p. 111–135.
- V. E., KuzikovskiiA. B. Zuev, V. A. Pogodaev, and L. K. Chistyakova, "Thermal effect of optical radiation on water droplets," Dokl. Akad. Nauk SSSR 205 (5), 1069–1072 (1972).
- M. G. Markov, Candidate's Dissertation in Mathematics and Physics (Institute of Physics and Power Engineering, Obninsk, 1985).
- A. P. Prishivalko, *Optical and Thermal Fields inside* Light Scattering Particles (Nauka i tekhnika, Minsk, 1983) [in Russian].
- 39. C. F. Bohren and D. R. Huffman, *Absorption and Scattering of Light by Small Particles* (Wiley, New York, 1983).

- 40. V. E. Zuev, B. V. Kaul', I. V. Samokhvalov, K. I. Kirkov, and V. I. Tsanev, *Laser Sounding of Industrial Aerosols* (Nauka, Novosibirsk, 1986) [in Russian].
- S. A. Beresnev, V. T. Chernyak, and G. A. Fomyagin, "Kinetic theory of photophoresis," Teplofiz. Vysokikh Temp. 26 (1), 120–130 (1988).
- 42. V. Chernyak and S. Beresnev, "Photophoresis of aerosol particles," J. Aerosol Sci. **24** (7), 857–866 (1993).
- J. Haywood and O. Boucher, "Estimates of direct and indirect radiative forcing due to tropospheric aerosols: A review," Rev. Geophys. 38 (4), 513–543 (2000).
- 44. S. A. Beresnev, F. D. Kovalev, L. B. Kochneva, V. A. Runkov, P. E. Suetin, and A. A. Cheremisin, "On the possibility of particle's photophoretic levitation in the stratosphere," Atmos. Ocean. Opt. **16** (1), 44–48 (2003).
- 45. S. A. Beresnev, L. B. Kochneva, P. E. Suetin, V. I. Zaharov, and K. G. Gribanov, "Photophoresis of atmospheric aerosols in the Earth's thermal radiation field," Atmos. Ocean. Opt. 16 (5-6), 431–438 (2003).
- 46. S. A. Beresnev, L. B. Kochneva, V. I. Zaharov, and K. G. Gribanov, "Photophoresis of soot aerosol in the Earth' thermal radiation field," Opt. Atmos. Okeana 24 (7), 597–600 (2011).

Translated by O. Bazhenov