Structural deviations in secondary phloem of young shoots of *Spiraea beauverdiana* near magma volcanoes

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**Abstract**

We performed a comparative analysis of the internal structure of the secondary phloem of one, two and three-year-old stems of *Spiraea beauverdiana* growing in extreme conditions of solfataric fields of Golovnin Volcano caldera and Mendeleyev Volcano and in normal conditions. The combination of environmental factors in conditions of solfataric activity, such as high temperatures in the soil and in the near-surface air, as well as saturation with gases toxic to plants, rare elements accumulating in the nearby substrate, and lack of soil moisture, interfere with normal phellogen and cambium activity. Deviations from the normal structure involve changes in the following parameters of the internal structure of a year-old stem of *S. beauverdiana*. Secondary phloem parameters in the studied habitats are normal, except for the length of the segments of sieve tubes, the height of single-row rays, the length of parenchymal girder; these are shorter in *S. beauverdiana* stems from volcanos. At two and three years of age in volcanic conditions we see reduction in the width of the secondary phloem (both conductive and non-conductive) and the diameter of the segments of sieve tubes. In samples from Golovnin Volcano we see reduction in tangential diameter, while in the samples from Mendeleyev Volcano it’s the radial diameter. We also see reduction in the height of multiple-row rays. At that age we see changes in the structure of the radial parenchyma; namely, we find no double-row rays in samples from Golovnin Volcano caldera. One of the signs of impact of volcanic activity on the bark structure is development of non-specific anomalies in the internal structure of the *S. beauverdiana* bark, namely, in the outer bark, or in deeper layers, such as the secondary phloem. That causes sclerification and dilatation of parenchyma, and multiple layers in some tissues.

1. **Introduction**

Vegetation of the Kuril Islands is influenced by complex and very unique natural conditions. One of the main factors impacting the plants is current volcanic and post-volcanic activity [1–2], as well as the impact from the cold of the Sea of Okhotsk and the Pacific [3]. Post-volcanic activity creates special landscapes with sufficient deficiency of soil moisture, high concentrations of salts of heavy metals, sulfur compounds, and high concentrations of sulfur oxides, nitrogen and other substances in the near-surface air [4]. Woody plants growing in these conditions have a whole set of adaptation mechanisms allowing them to survive in such harsh areas.

The object of this research is *Spiraea beauverdiana* S.K. Schneid. (Rosaceae Juss.), a woody plant up to 60 cm high, with fringed or bare young reddish-brown shoots. The bark of a multi-year shoot is
brown. Its flowers are white, pinkish sometimes [5]. Depending on the environment, this species has two life-forms: a deciduous brush (up to 1 m tall) and a deciduous low shrub. The distribution area of the species includes Siberia, the Russian Far East, China, and Japan. The northern boundary of the area is in the Arctic latitudes [6]. *S. beauverdiana* grows on rocks and rocky slopes, in the shrub tundra and herb meadows, in the mountain forests and sparse forests [5].

The purpose of this research is to make a comparative analysis of the internal structure of the secondary phloem of young shoots of *Spiraea beauverdiana* growing in solfataric fields of active volcanoes (Golovnin and Mendeleyev Volcanoes) and in normal conditions on Kunashir Island.

As a connecting link in distribution of carbon in plants, the phloem and its network of living channels (sieve tubes) are at the heart of the mechanisms distributing the plant’s resources. Understanding of the functioning of the phloem of a woody plant, including cenose-forming species (trees, brush, and low shrub) has a great environmental and agricultural value. Using optical and electronic microscopy, we obtain data on the structure of segments of sieve tubes of plants taken from various areas, on their structural relations with satellite cells, the axial and radial parenchyma, which expands and clarifies our knowledge of the structure of the long-range phloem network in woody plants [7].

2. Materials and methods

We took samples of one, two and three-year-old shoots of *S. beauverdiana* from three plants growing in the northern section of the Central Eastern solfataric field of Golovnin Volcano caldera, in the North-Eastern solfataric field of Mendeleyev Volcano, and in the bushy bamboo typical for that species inside the caldera of Golovnin Volcano (Kunashir island). We select and preserve shoot samples for anatomical analysis in line with the standard guidelines [8–10]. Brief geobotanical descriptions were made for, and *Spiraea beauverdiana* samples were taken from, 10×10 m sampling areas.

In the northern section of the Central Eastern solfataric field of Golovnin Volcano caldera there are a number of boiling potholes and active solfataras. The solfataric gases can be as hot as 90–100°C. The thermal springs contain an increased concentration of microelements, such as Pb–Cd and Rb–As. Gas of the thermal springs contains mostly carbon dioxide and hydrogen sulfide [11]. In these conditions, *S. beauverdiana* can be found as part of thin vegetation. Loose groups of *Reynoutria sachalinensis* (Fr. Schmidt) Nakai and very close-knit bushes of *S. beauverdiana*, *Ledum hypoleucum* Kom., and *Empetrum sibiricum* V. Vassil. not taller than 10–15 cm grow 10–15 m away from the heart of the solfataras. In these conditions, *S. beauverdiana* is represented by its low shrub life form.

In the North-Eastern solfataric field of Mendeleyev Volcano there are many solfataras with temperatures up to 99.6°C, and several places where solfataric gas condensate seeps out in the stream creeks. The rocks here are altered and enriched with sulfides of metals as a result of hydrogen sulfide and sulfur dioxide coming to the surface. The whole surface of the field is covered with a crust of sulfur [11]. The vegetation around the field grows in open communities and standalone groups of plants. *S. beauverdiana* can be found in plant communities of mountain pine and bamboo (*Pinus pumila*, *Sasa, Hydrangea paniculata*, *Menziesia pentandra*, *Ledum hypoleucum*) or brush, sword grass and knotweed (*Ledum hypoleucum*, *Gaultheria miqueliana*, *Sasa, Miscanthus sinensis, Reynoutria sachalinensis*).

Samples of *S. beauverdiana* growing in typical conditions were collected inside the caldera, but far from the center of solfataric activity (about 1 km away). Here the plant is found among mountain pines and bamboo brush (*Ledum hypoleucum*, *Spiraea beauverdiana*, *Empetrum sibiricum*).

We made a statistic analysis of 13 quantitative parameters of the secondary phloem of *S. beauverdiana* for every habitat. Sample size for each parameter was at least 30 measurements. When analyzing parameters of tissue and cells for one, two and three-year-old stems, we calculated the sample average, maximum, and minimum values, variation coefficient, the standard square deviation, expectation for the sample average (for confidence figure of 95%).
3. Results and discussion

Cross-sectionally, the stem of *S. beauverdiana* has four or five sides. The central cylinder is formed around the procambial ring. Bark tissue composition changes significantly over the first vegetation season, due to early generation of phellogen in the deep layers of the bark and subsequent degeneration of the primary tissues. At the end of the first vegetation season, bark tissues located outside of the periderm die and get deformed, but remain on the stem. The endoderm is likely formed after suberinization of the phellem. Therefore, at the end of the vegetation season the bark of the *S. beauverdiana* stem contains the following layers, from the outside to the center: deformed epidermis; deformed cortex, including collenchyma, ground parenchyma, and endodermis; outer bark; protophloem, protophloem fibers and sclereids; metaphloem and secondary phloem [12]. In a year-old stem the secondary phloem includes only the conductive phloem made up of sieve tubes and companion cells, the axial and radial parenchyma. Sieve tubes in the cross-section are diffuse or found in small groups of two or three. The axial parenchyma is diffuse [13].

Comparative studies of the structure of secondary phloem of young stems of *S. beauverdiana* in contrasting environmental conditions revealed a number of structural peculiarities. In a year-old stem from the solfataric field of Mendeleev Volcano, the width of the conductive phloem is 18% more (21.9±1.46 microns) than the norm (18.5±0.72 microns). And in the solfataric field of Golovnin Volcano caldera the width of the conductive phloem is close to typical values (figure 1a). In a two or three-year-old stem the secondary phloem includes conducting and non-conducting phloem. At that age, in volcanic conditions, the width of conductive and non-conductive secondary phloem decreases. Conductive phloem is reduced by 42% at Golovnin Volcano (16.1±0.89 microns), and by 23% at Mendeleev Volcano (18.5±1.00 microns) (figure 1a). Non-conductive phloem reduced by 57% at Golovnin Volcano (14.2±0.84 microns), and by 27% at Mendeleev Volcano (17.5±1.80 microns), while the norm is 22.3±1.76 microns (figure 1b).

In a year-old stem the radial and tangential diameters of the sieve tube segments are within normal (figure 1c, d). At two and three years of age, under stress, we see the radial diameter in samples from Mendeleev Volcano reduced by 24% (3.7±0.17 microns) (figure 1c) and tangential diameter in samples from Golovnin Volcano reduced by 16% (5.1±0.35 microns) (figure 1d) as compared to the norm (4.6±0.31 microns and 5.8±0.29 microns, respectively).

In a year-old stem, the segments of sieve tubes in conditions of the solfataric field of Mendeleev Volcano are 27% shorter (135.3±15.11 microns) that the norm (172.2±15.31 microns). In two and three-year-old stems in extreme conditions that parameter remains within the norm (figure 1e).

The radius in the phloem of year-old stems from the solfataric field of Golovnin Volcano and in typical conditions are only single-row and homocellular, and double-row ones can be found in the solfataric field of Mendeleev Volcano. At two and three years of age, the structure of the radial parenchyma changes, and there are no instances of double-row radius in samples from Golovnin Volcano caldera. The total number of phloem rays in one, two and three-year-old stems in stress conditions is normal. In a year-old stem of *S. beauverdiana* the height of single-row rays in conditions of the solfataric field of Mendeleev Volcano is 39% less (169.9±16.45 microns) than the norm (236.0±17.83 microns). In two and three-year-old stems this value is close to the typical conditions for both habitats (figure 1f). Multiple-row rays are found only in two or three-year-old stems. In two and three-year-old stems the multiple-row rays are shorter in both extreme habitats. In samples from Golovnin Volcano they are 25% shorter (214.3±15.39 microns), and in samples from Mendeleev Volcano they are 22% shorter (220.4±21.61 microns) than the norm (268.7±20.35 microns). The width of multiple-row rays in two and three-year-old shoots in the solfataric field of Golovnin Volcano is 24% less (18.2±1.56 microns) than the norm (22.6±1.51 microns). In samples from Mendeleev Volcano the value is normal.

The parenchymal girder in a year-old stem in extreme conditions of Golovnin Volcano is 31% shorter (82.7±5.15 microns), and in two and three-year-old stems 14% shorter (113.1±5.11 microns) than the norm (109.0±6.55 microns and 129.6±4.46 microns, respectively). In one, two and three-year-old shoots in the solfataric field of Mendeleev Volcano the value is close to that for typical conditions.
Figure 1. Anatomical features of the bark of 1 and 2–3 year old stems *Spiraea beauverdiana*. a – conductive phloem width; b – non-conductive phloem width; c – radial diameter of sieve tubes; d – tangent diameter of sieve tubes; e – sieve-tube element length; f – ray uniseriate height.  

Golovnin Volcano caldera (typical conditions); Central Eastern solfataric field of the Golovnin Volcano caldera; North-East solfataric field of the Mendeleyev Volcano.

One of the signs of impact of volcanic activity on the bark structure is development of non-specific anomalies in the internal structure of the *S. beauverdiana* bark, which develop most actively at a young age (three to five years) and reach maximum values in boughs by eight years [12]. We found anomalous areas in young stems of *S. beauverdiana* from solfataric fields of the caldera of Golovnin Volcano and Mendeleyev Volcano. Most commonly, we found that young stems have structural
anomalies of the outer bark, such as multiple layers of phellem and phelloderm. Secondary phloem anomalies found in young stems of *S. beauverdiana* from solfataric fields of the researched volcanoes are mostly represented by small areas where axial and radial parenchyma includes groups of large sclereids. Tangential and radial sizes of such cells are two or three times bigger than normal tissue. Rays in such sections are heterocellular and dilated, and sieve tubes are deformed by the overgrown sections of parenchyma [14–15].

Our findings match the discovered trends of structural changes of secondary phloem of *Betula ermanii* Cham. in conditions of solfataric fields and fumarole fields of Baransky Volcano on Iturup island and *Toxicodendron orientale* Greene in conditions of Mendeleyev Volcano on Kunashir island [4, 16–18]. We saw similar results in year-old stems of *Betula ermanii* in conditions of Starozavodskoye solfataric field of Baransky Volcano, where the conductive phloem is wider than normal. The same trend was observed in year-old stems of *Toxicodendron orientale* in conditions of Verkhnedoctorskoye hot springs at Mendeleyev Volcano [4]. This response is probably typical for many woody plant species growing in such extreme conditions. We think that further research is necessary for other species and other active volcanoes.

4. Conclusion
The common trend in structural changes of the secondary phloem in conditions of solfataric fields of Golovnin and Mendeleyev Volcanos is adaptive reduction of conductive elements while maintaining their structural connection to parenchyma. We believe these peculiarities of conductive phloem to be adaptive in nature, as a response to the extreme conditions of gas and hydrothermal fields in volcanic landscapes. Perhaps lack of water due to high concentration of salts interferes with carbon transportation in the phloem. We think that development of anomalous areas of this tissue is the extreme form of structural and functional changes in the phloem in volcanic conditions.

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