

On Adaptations of Trees and Shrubs in the North of the Russian Far East

T. A. Moskaluk

Botanical Garden–Institute, Far East Division, Russian Academy of Sciences,
ul. Makovskogo 142, Vladivostok, 690028 Russia
e-mail: tat.moskaluk@mail.ru

Received May 5, 2006

Abstract—Specific ecological features of trees (*Chosenia arbutifolia* and *Betula lanata*) and shrubs (*Pinus pumila* and *Duschekia fruticosa*) at the northern limit of their distribution are compared. New biomorphological adaptations of these species under extreme conditions are described.

DOI: 10.1134/S106741360802001X

Key words: *Betula lanata*, *Chosenia arbutifolia*, *Pinus pumila*, *Duschekia fruticosa*, ecology, biomorphological adaptations, northern Far East.

Problems of plant adaptation to severe environmental conditions have long attracted the attention of researchers (Tikhomirov, 1949; Grosset, 1959; Kryuchkov, 1968; Mazurenko, 1986; etc.). The most diverse adaptive features develop in plants growing at extreme points of their ranges, and, therefore, species growing at the northern limit of forest vegetation are of special interest. In the Russian Far East, this concerns primarily *Chosenia* (*Chosenia arbutifolia* (Pall.) A. Skvorts.), stone birch (*Betula lanata* (Rgl.) V. Vassil.), mountain pine (*Pinus pumila* Rgl.), and shrub alder (*Duschekia fruticosa* (Rupr.) Pouzar).¹

Their ecological features have been studied fairly thoroughly (Kolesnikov, 1937; Vasil'ev, 1941; Grosset, 1959; Kabanov, 1972; Molozhnikov, 1975; Mezheny, 1976; Mazurenko and Moskaluk, 1991; Khomentovskii, 1995; Shamshin, 1999; etc.). However, studies on the cenotic structure of northern forests resulted in the discovery of previously unknown biomorphological adaptations in these species. In this paper, I describe these new adaptations and analyze ecological similarities and differences between these species that allow them to optimize their relationships and avoid competition while growing together.

MATERIAL AND METHODS

The bulk of material was collected in the northern Sea of Okhotsk region (the Yana, Chelomdza, and Dukcha river basins), the Upper Kolyma region (the Buyunda and Sibit-Tyellakh river basins), and on the

Chukchi Peninsula (the Bol'shoi Keperveem River basin).

The northern Sea of Okhotsk region is the most forested part of Magadan oblast. According to climatic zoning (Klyukin, 1970), it lies in the area of tundra and forest–tundra climate (within the forest zone). This is a moderately continental climate with cold, snowy, and windy winters; long, cold springs; short, cool summers; and warm, windless autumns. The monthly average air temperatures in January and July are –20.8 and 12.8°C, the sums of temperatures above 5 and 10°C reach 1200–1400 and 750–1010°, respectively; the number of days with above-zero temperatures is about 150; and the annual amount of precipitation averages 520–700 mm. More than 60% of this amount falls in the warm period, which is indicative of a monsoon climate type.

The main study site was on the southern–southwestern macroslope of the Khasynskaya Ridge (250–500 m a.s.l.), which forms the left boundary of the Dukcha River valley in its middle reaches (30 km northwest of Magadan). In northern latitudes, site conditions are known to be most favorable on southern slopes, where the sum of above-zero temperatures is 400–600° higher than on northern slopes and 200–300° higher than in river valleys (Khlynovskaya, 1982), and moisture supply is 1.5–2 times more abundant (up to 700 mm per year) than in slopes protected from monsoon winds.

Forests on southern slopes are characterized by the richest species composition, including the group of edificator species. The macroslope used as the study area was previously covered by larch–stone birch forests with an undergrowth of *P. pumila* or *D. fruticosa* (the latter is common in creek valleys and depressed slope discontinuities), sometimes with *Sorbus sam-*

¹ Latin names are given according to the monograph *Sosudistye rasteniya sovetskogo Dal'nego Vostoka* (Vascular Plants of the Soviet Far East), 1985–1996.

bucifolia Cham. et Schlecht. and *Betula middendorffii* Trautv. et Mey.

To date, the vegetation on the slope has radically transformed under anthropogenic impact. Its pattern and degree of development are determined by conditions of moisture supply, which markedly vary depending on the degree of the slope and microrelief. Xeromorphic areas with stony soils, convex surface, and a slope of 30–40 degrees have a discrete pyrogenic plant cover formed by small fragments of subgoltsy mountain pine cenoses alternating with mineralized areas in which *B. lanata* regenerates actively.

In flat areas and depressions with sufficient moistening and relatively fertile soils, a continuous plant cover with a tree layer composed of *B. lanata* has developed over the same period as in concave areas. Small fragments of weakly disturbed overmature stone birch forest with larch and undergrowth of *P. pumila* or *D. fruticosa* survive only in creek valleys and at the boundary between the steep part (near the watershed) and relatively flat part of the slope. *Pinus pumila* and *D. fruticosa* are coedificators in these stands, along with stone birch.

Chosenia was studied in floodplains of the Yana, Chelomdzha, Kava, and Dukcha rivers and in areas of depleted placer deposits in the Bol'shoi Keperveem valley.

Ecological features of forest-forming species were studied in permanent and temporary test plots and during route surveys. Taxonomic and geobotanical descriptions of test plots were made according to methodological guidelines by Sukachev and Zonn (1961) and Utkin (1974). In particular, the complete floristic composition and cenotic structure of vegetation were analyzed. Special attention was paid to the study of ecobiomorphs of edificator species.² The patterns of branching and shoot formation in plants of different ages growing under different conditions were described, and root systems were dug out for analysis (in *P. pumila* and *D. fruticosa*). During weekly phenological observations, abnormalities in the seasonal development of individual organs in dominant and indicator species were recorded.

RESULTS AND DISCUSSION

In the course of evolution, all forest-forming species considered in this study have acquired specific features allowing them to grow successfully under conditions of the extreme North. *Chosenia arbutifolia*, *B. lanata*, *P. pumila*, and *D. fruticosa* have a number of features in common: they are photophilous, hygrophilous, relatively cold-hardy, indifferent to soil fertility, and intolerant of stagnant overmoistening. On the other hand, they differ in responses to the same ecological factors.

² Ecobiomorphs are species life forms existing under certain ecological conditions and differing from each other in biomorphological characters (Zhmylev et al., 2002).



Fig. 1. Nonuniform leaf opening in the crown of a tree growing in a convex area on the southern slope.

Betula lanata and *P. pumila* have more stringent requirements for air humidity, whereas *Ch. arbutifolia* and *D. fruticosa* are more sensitive to soil moisture content. With respect to sensitivity to overmoistening, they may be arranged in the following series: *Ch. arbutifolia*, *D. fruticosa*, *B. lanata*, and *P. pumila*. *Betula lanata* and *D. fruticosa* prefer more fertile soils than do *Ch. fruticosa* and *P. pumila*. Their requirements for light also differ, being especially high at a young age in *Ch. arbutifolia*, at a mature age in *P. pumila*, and remaining high throughout life in *B. lanata*; *D. fruticosa* is less shade-tolerant than *P. pumila*.

Betula lanata, together with *P. pumila*, forms the upper forest belt in southern regions of the Far East. In Magadan oblast, it grows on southern slopes and in river valleys. This species is more thermophilic than *P. pumila*, and its range expands no farther than to the watershed of rivers of the Sea of Okhotsk basin. Stone birch forests are the main component determining the unique pattern of vegetation in the northern Sea of Okhotsk region (Khokhryakov, 1976; Shamshin, 1999).

The buds and shoots of *B. lanata* are covered with down, and this cover is denser than in other stone birch species. This character is regarded as an adaptation to cold, primarily to the impact of frosty winds in winter



Fig. 2. Medium-aged cowberry–herb–sedge stone birch forest with mountain pine in a gully.

(Vasil'ev, 1941; Kabanov, 1972; etc.). As a rule, leaf blades and stalks are also downy. This character is expressed more strongly under more severe environmental conditions.

Phenological observations in permanent plots (1987–1990) revealed some other features of *B. lanata*. It was found that phenophases in this species did not coincide in two adjoining plots with regenerating stone birch forests of medium age growing in the middle part of the slope (320–380 m a.s.l.). In a “dry” *green moss–cowberry stone birch forest with mountain pine* in a convex part of the slope (more rapidly warmed in spring), the leaves of *B. lanata* were more densely covered with down and opened 5–7 days earlier than in a “moist” *cowberry–mixed herb–sedge stone birch forest with mountain pine* growing in a gully.

In addition, it was found that leaves in some *B. lanata* trees were fully open in the lower part of the crown but just beginning to open in its upper part (Fig. 1), with the difference between “phenophases” in the same tree reaching one week. Such trees usually grew in places where the ground air layer remained warmer, namely, in microdepressions or in areas protected from northerly winds by mountain pine thickets. The same spatial pattern was characteristic of change in leaf color in autumn (in both young and mature trees).

Crookedness of stems is a distinctive species character of *B. lanata* (Elagin, 1961; Kabanov, 1972; etc.). Specialists consider it adaptive and indicate many factors that may be responsible for the bending of stems and branches. It should be noted that these factors may differ even within a small area.

In a *herbaceous stone birch forest with brush alder, mountain pine, and larch* growing in the zone of slope discontinuity (between its steep watershed part and relatively flat upper part), *B. lanata* trees usually have lower parts of the stems crooked toward the base of the slope. This is explained by a large amount of snow (its depth reaches 1.5–1.7 m), which slides down the slope during warm spells and the spring thaw. Trees in the stone birch forest growing in the gully are not crooked, as snow depth there does not exceed 1 m and the degree of slope is small (Fig. 2).

Under relatively favorable wintering conditions, crooked stems are characteristic of *B. lanata* trees growing in dense clusters, but their shape differs from that developing under the load of sliding snow. In the largest cluster (26 trees 5.8–6.5 m high and 8.0–11.9 cm in diameter) of the moist stone birch forest, tree stems are straight at the base but divide into two or more stems at a height of 1.0–1.3 m, bending toward the periphery of the cluster. In this case, crookedness is apparently due to light deficiency within the cluster, where crown density is high and the mountain pine undergrowth is well developed.

This agrees with Ermakov's (1986) opinion that stone birch is tolerant of long-term shading but, as soon as a gap appears in a dense canopy, its shoots immediately change the direction of their growth and extend toward this gap, with shoots receiving more light growing more rapidly. As a result, skeletal branches acquire a crooked shape.

In prominent microrelief elements where a thin soil cover is dry, the causes of stem bending are different.



Fig. 3. Shrublike ecobiomorph of *Betula lanata* under extreme growing conditions.

High winds blow the snow away from such sites and leave young birch trees unprotected from abrasion by snow crystals, frostbite, and sunburn, which damage their bark above the snow crust. As a consequence, the stem gradually bends in its lower segment and remains crooked.

Kryuchkov (1976) described such a mechanism of crooked stem formation for *Betula tortuosa* in the north of the Kola Peninsula. He notes that stem bending in that species is observed upon even slight deterioration of growing conditions. When this deterioration is significant, apical buds or even parts of the shoot die, which leads to activation of numerous dormant buds at the stem base and above it. In this study, the same was observed in the dry stone birch forest: birch seedlings branched, and more than half of older trees had two to four slanting stems crooked at the base (Fig. 3). No multistemmed trees were found in creek valleys, gullies, and other sites protected from wind and sufficiently supplied with moisture.

One more biological feature indicative of the very high ecological flexibility of *B. lanata* was revealed in an overmature *herbaceous stone birch forest with mountain pine* (Fig. 4). A small stand of this forest type has survived in the upper reaches of a creek valley at an elevation of 450–480 m a.s.l. Old birch trees have knotty stems and spreading crowns with the lowest branches located at a height of 3–4 m, immediately above the mountain pine canopy. In the oldest tree, the stem at a height of 3.5 m was divided into four daughter stems. In the year of observation, one of these stems broke slightly above the fork and exposed an adventitious root with branching lateral rootlets lying in rotten wood (Fig. 5). The root was 70 cm long and its proximal diameter was 5 cm. The broken stem did not separate from the tree, and its crown (lying on the ground) remained green for several years.

It may well be that this case is not exceptional and such roots are also formed in the stems of other overmature trees, supplying them with additional nutrients from their own decaying wood and thereby prolonging their life.

Chosenia arbutifolia expands northward farther than other tree species (up to 72° N) but is confined to talik zones in river floodplains. Pouring rains resulting in floods are usual in the Far East during the summer season. Such floods have a devastating impact on mountain areas, resulting in riverbed scour and formation of numerous sand-pebble spits and islands, which are ideal ecotopes for this species (Kolesnikov, 1937; Huang and Shao, 1987).

Chosenia has a powerful root system, a xeromorphic type of seminal leaves and the first true leaves (Fig. 6), and a rosette pattern of shoots (Fig. 7), which account for a low resistance to water flow during the floods. These adaptations to growing in pebbly floodplain areas manifest themselves beginning from the earliest stages of its ontogeny. When *chosenia* seedlings and young plants firmly establish themselves in the substrate, they begin to perform their environment-forming function.

Plants at the age of 4–5 years assume a shrublike life form and actively accumulate alluvial material around them. As a fertile soil layer is formed and cenoses escape the impact of floods, the plant increment sharply increases up to 1.5 m per year. At the age of 15–20 years, *chosenia* is a typical mesophyte with ribbons of peeling bark, a purplish wax coating on whiplike shoots, and a deep purplish red color of leading shoots. These morphological characters account for protection of cambial tissues in the stem and young shoots (Shamurin, 1966; Savile, 1972), providing for a high cold hardiness of adult trees.

Two interesting adaptations were revealed in *chosenia* plants growing on pebble dumps in the zone of



Fig. 4. Overmature herbaceous stone birch forest with mountain pine in a creek valley.

depleted placer deposits near Bilibino (the Chukchi Peninsula). In the period of summer rains, environmental conditions on these dumps are similar to those in pebbly floodplains and numerous chosenia seedlings appear there in the period of seed dispersal. Most of the seedlings die, but single surviving individuals develop within 10–12 years into densely leaved plants several meters high. Many of them are of a specific tumbler-shaped ecobiomorph (similar to the cup-shaped shrub-like life form) with four or five (rarely, six or seven) stems developing from substitution shoots of the first two years of life. As a rule, the center of the “tumbler” is marked with a thin stump, the remnant of the dead primary shoot. Unlike in *B. lanata*, whose stems rise obliquely, *Ch. arbutifolia* stems are initially plagiotropic (lie on the ground) and then, at a distance of 10–15 cm from the center, sharply bend and grow orthotropically. It appears that the plagiotropic growth of chosenia at the stage of rosette ontobiomorph is an evolutionarily established character that should be expressed in any plant, irrespective of growing conditions.

Condensing atmospheric moisture is the only source of water for chosenia plants growing on the dumps. The development of several equivalent stems provides for the optimal distribution of assimilatory systems in humid near-ground air layers, thereby alleviating water deficiency. Moreover, as the protective wax coating of chosenia stems and shoots falls to the ground, its surface area under the crown is blackened and, hence, the temperature near the stem is several degrees higher than in open areas (Papernov and Zamoshch, 1983). Both the development of the tumbler-shaped ecobiomorph and the blackening of the ground surface under the crown may be regarded as ecological adaptations of chosenia aimed at optimizing conditions of heat and moisture supply in its habitats.

Pinus pumila is a component of the subgoltsy vegetation belt throughout the Far East. In the north, it grows on mountain slopes and in river valleys. In the coastal zone, it forms impenetrable thickets on slopes facing the sea. In the cold season, plants are buried



Fig. 5. Adventitious root at the base of crown in an overmature *Betula lanata* tree.

under snow and escape the desiccating and freezing impact of winter winds.

Depending on environmental conditions, *P. pumila* trees may have a cup-shaped, prostrate, or shrublike life form. All these ecobiomorphs occur in the study area. In the subgoltsy belt and in burned-out areas, this species either grows as separate cup-shaped shrubs or forms thickets. The plants have dense, compact crowns

and thick needles. The age of needles in burned-out areas is 4–5 years, being 1–2 years smaller than under the forest canopy.

Pinus pumila poorly tolerates even slight shading, and the pattern of its cenopopulations in the forest sharply differs from that in open areas. In the forest, it neither forms thickets nor bears fruit, and shoots with needles concentrate in the upper one-third of the crown (shoots aged 6–7 years are also needled, though thinly). The shoot increment in length is insignificant, several times smaller than in plants growing in well-illuminated areas.

According to Khomentovskii (1995), the cup-shaped life form of *P. pumila* plants provides for the most effective utilization of solar radiation and they tend to assume it whenever possible. Specialists differ in their opinions concerning the origin of this form. Some authors consider that it is due to simultaneous germination of a pile of seeds stored by the nutcracker (Grosset, 1959; Tikhomirov, 1949; Kotlyarov, 1973; etc.) or seeds from the same fallen cone (Starikov, 1958). In due time, growing shoots develop into shrubs of different forms, including cup-shaped shrubs with stem bases accreting to each other. According to Mezhenyi (1976), the shoot system of a cup-shaped shrub is formed by one individual, as only one or two living plants remain in a bunch of seedlings after 2–3 years. Lower shoots of the surviving plant begin to grow very actively, giving rise to skeletal branches of the future shrub. In the study area, cup-shaped shrubs were formed mainly in the latter way, beginning from the age of 5–7 years.

The ecotone between forest and burned-out area is occupied by single *P. pumila* plants; in the forest, they



Fig. 6. (a) Seedling and (b) two-year-old plant of *Chosenia arbutifolia*.



Fig. 7. Three-year-old *Chosenia arbutifolia* plant of a rosette ecobiomorph.

concentrate in better illuminated and dry habitats. The youngest individuals are five years old and only 0.32 m high. All plants no higher than 60 cm have one or two axial shoots; “shrubs” ranging in height from 60 cm to 2 m had three to four axial shoots; and larger shrubs (above 2 m) had 5–10 or, in some cases, even 14–17 axial shoots. These shoots grow obliquely; their bases lie on the ground and are gradually being covered with litter and overgrown with moss. If the base of the shrub occasionally remains bare (for unknown reasons), it becomes evident that the plant is a shrublike tree and its shape resembles a goblet rather than a cup (Fig. 8).

In forest cenoses with a degree of crown closure exceeding 0.7, the prostrate life form prevails in *P. pumila*. The main skeletal axis (stem) is plagiotropic, with adventitious roots extending from it at the sites of contact with the soil. Skeletal shoots grow orthotropically and reach 2.5 m in height. As the stem is completely covered with the litter and ground vegetation, it appears that each shoot is an individual plant. In places, stems of different plants lie so close together that their bases are inaccessible and their shoots form a dense thicket, regardless of the low needle density.

It is known that abnormally high temperatures in the summer–autumn period lead to disturbances in the seasonal cycle of perennial plants, including secondary leaf budding, blossoming, and the onset of shoot growth. Many dwarf shrubs of the heath family in the far north grow in several increments per season. Accelerated progression through phenophases is regarded as a component of an adaptive strategy that allows plants to complete their developmental cycle in time under extreme conditions (Mazurenko, 1986).

The insertion of secondary growth phases into the developmental cycle is common in *P. pumila*, espe-

cially in plants growing on southern slopes. The magnitude of the secondary increment differs depending on conditions in ecosystems. In the study period, it averaged 1.0 cm in areas with a convex surface and reached 2.0 cm in the gully.

Between 1985 and 1990, the secondary growth of current-year shoots (auxiblasts) was most active in 1988. The summer of that year was warm and dry, with



Fig. 8. *Pinus pumila* plant of unusual goblet-shaped, or shrublike tree growth form.



Fig. 9. Stems of *Duschekia fruticosa* are crooked in the direction of snow sliding down the slope.

unusually high temperatures at the end of the season. In the dry stone birch forest, the growth of auxiblasts in *P. pumila* ceased by the end of the first ten-day period of July, being followed by the accelerated growth of needles, formation of apical buds, and lignification of shoots. By the end of July, the needles grew to their definitive length (6.0–6.5 cm) and the plants finally shed cover scales protecting developing needles from excessive heating or cooling. These scales allow *P. pumila* to withstand late frosts occurring in the south of Magadan oblast even in late June (whereas the larch often loses all needles after such frosts). New needles in *P. pumila* begin to grow in mid-June, and their clusters remain wrapped in cover scales for two to three weeks.

In early August, after tissue lignification, elongation of wintering buds was observed in the best-developed shrubs. The secondary apical increment of axial shoots was 1.0–1.2 cm in August and reached 2.0 cm by mid-September, averaging 1.0–1.5 cm.

The seasonal development of the *P. pumila* cenopopulation in the moist stone birch forest followed the same pattern, but the onset of each phenophase was delayed for several days because of later snow melting

and lower temperatures. Nevertheless, the secondary shoot increment averaged 2 cm in late August and became 1.5 cm greater by the beginning of September. In one shrub, the total increment reached 4 cm. This shrub grew in an open, flat area 2 m west of a cluster of birch trees (which protected it from wind) and south of a small bench, which served as a screen reflecting solar heat. The abundant growth of sedges (*Carex pallida* C.A. Mey. and *C. vanheurckii* Muell. Arg.) and tall herbs around this shrub was indicative of optimal soil moistening.

In the overmature stone birch forest growing in the upper reaches of a creek valley, no secondary increment in *P. pumila* was recorded during the whole observation period. A probable explanation is that the thick *P. pumila* undergrowth in this forest type is strongly shaded by tree crowns and looks suppressed.

Plant tissues formed in autumn usually fail to “mature” and die with the onset of winter, as is the case with *Loiseleuria procumbens* (L.) Desv. (Mazurenko, 1986). In the forests studied, secondary auxiblasts in *P. pumila* had not yet lignified by the winter of 1988/1989, but they successfully overwintered and began to grow the next spring. Unexpectedly, the boundary between shoot parts formed in autumn and in spring was undetectable: there was no false tree ring or constriction allowing differentiation between the primary and secondary increments. In the next year, such shoots overwintered in the same way.

Unfortunately, it was impossible to continue observations on the growth and development of secondary shoots in *P. pumila*, but the available data provide a basis for regarding the above phenomenon as one more adaptation of this species to severe conditions in its habitats.

Duschekia fruticosa, along with other plants accompanying *B. lanata*, is a major diagnostic species of the Far Eastern floristic complex in the northern Sea of Okhotsk region. It is a component of undergrowth in larch–stone birch forests on southern mountain slopes. On the Sea of Okhotsk coast, this species forms dense and tall thickets in the subgoltsy belt and on slopes facing the sea, similarly to *P. pumila*. The specific structure and similarity of *P. pumila* and *D. fruticosa* cenoses provided a basis for classifying them as a specific type of vegetation named prostrate forests (Sochava, 1956; Kolesnikov, 1961).

Both these species are thermophilous and photophilous, but *D. fruticosa* has high requirements for soil moisture and fertility. This is why these species growing in the same cenosis are segregated from each other in different microhabitats and form individual cenotic elements. *Duschekia fruticosa* prefers flat areas and depressions with periodic moistening and fertile soils, whereas *P. pumila* is confined to microelevations. Their specific distribution on the slope, with plants arranged in narrow bands and “tongues” (characteristic primarily of *P. pumila*), is determined by the distribution of microelevations and microdepressions extending downward,

along the flows of surface runoff, and reflecting the pattern of these flows.

Visual examination of large groups (clusters) of *D. fruticosa* may create a false impression that this species settles on microelevations. However, as follows from the results of excavations in such a cluster in a *herbaceous shrub alder–mountain pine stone birch forest with larch* growing in the subgoltsy belt, these microelevations are formed by dead basal parts of *D. fruticosa* stems, which gradually decompose, and become buried under plant litter, alluvium, and hillside waste, being finally overgrown by mosses and shade-tolerant herbage. The biomorph of *D. fruticosa* in clusters is similar to the prostrate biomorph of *P. pumila*, but the living plagiotropic part of the stem is several times shorter than in the latter. The place of establishment and true age of an individual *D. fruticosa* plant are impossible to determine even by means of most thorough excavation. It is also difficult to determine whether a given cluster is a clone with segregated stems (branches) or a group of individuals whose crowns and shoot systems merged with age.

Compared to *P. pumila*, *D. fruticosa* is less tolerant of growing together with other forest-forming species. It rarely occurs in dense clusters of stone birch and shrub alder, and plants growing there are poorly developed. No cases of *D. fruticosa* establishment within openings in *P. pumila* thickets have been recorded, although young and relatively small *P. pumila* shrubs grow within openings in thickets of *D. fruticosa* plants or under the peripheral parts of their crowns. Moreover, the crowns of these two species barely come in contact even in areas where they form a continuous undergrowth layer. *Duschekia fruticosa* may occur in the undercrown area near larch trees (at the periphery), but the growth of its thickets is possible only under the high crowns of old birch trees.

The crookedness of stems in *D. fruticosa* is manifested to even greater extent than in *B. lanata* growing in the same cenosis: all stems slant toward the base of the slope and are strongly crooked in the lower segment (Fig. 9).

CONCLUSIONS

The results of this study provide new evidence for the high ecological flexibility of forest-forming species *Betula lanata*, *Chosenia arbutifolia*, *Pinus pumila*, and *Duschekia fruticosa* under extreme growing conditions and for their effective adaptation to environmental changes at any age.

The most noteworthy adaptations are as follows:

(1) development of a cup-shaped shrublike ecobiomorph in young *Ch. arbutifolia* and *B. lanata* plants;

(2) development of adventitious shoots at the bases of skeletal branches and their growth within rotten stem wood in overmature *B. lanata* trees;

(3) nonuniform leaf opening in spring and change of leaf color in autumn at different levels of the same tree crown in *B. lanata*;

(4) the absence of frost damage to secondary shoot increments and of constrictions delimiting the zones of secondary (autumn) growth and subsequent spring growth of shoots in *P. pumila*; and

(5) the presence of different forms of stem crookedness explained by the effects of different factors in *B. lanata* trees growing on the same macroslope and even in the same ecosystem.

The similarity of adaptations to the limiting factor in different species has been revealed:

under conditions of acute moisture deficiency and intense insolation of habitats, all four species assume a cup-shaped shrublike ecobiomorph or a tumbler-shaped ecobiomorph, with the mechanism of its formation being independent of plant species;

under conditions of sufficient moisture supply and light deficiency, *P. pumila* and *D. fruticosa* are characterized by the same prostrate ecobiomorph with a plagiotropic stem–branch and orthotropic lateral shoots extending from it.

In complex cenoses, different forest-forming species are segregated in certain microhabitats that provide conditions satisfying their specific ecological requirements. This is especially distinct in the case of *P. pumila* and *D. fruticosa*.

REFERENCES

- Elagin, I.N., In Kamchatka Stone Birch Forests, *Priroda*, 1961, no. 1, pp. 106–108.
- Ermakov, V.I., *Mekhanizmy adaptatsii berezy k usloviyam Severa* (Mechanisms of Adaptation to Conditions of the North in Birch), Leningrad: Nauka, 1986.
- Grosset, G.E., Mountain Pine, *Byull. Mosk. O–va Ispyt. Prir., Otd. Biol.*, 1959, vol. 20, issue 12.
- Huang Pu-Hwa and Shao Zhong-Wen, Rare and Valuable *Chosenia arbutifolia* Trees, *G. North-East Forest. Univ.*, 1987, vol. 15, no. 1, pp. 1–6.
- Kabanov, N.E., *Kamennoberezovye lesa v botaniko-geograficheskoy i lesovodstvennoy otnosheniyakh* (Stone Birch Forests in Botanical–Geographic and Silvicultural Aspects), Moscow: Nauka, 1972.
- Khlynovskaya, N.I., *Agroklimaticheskie osnovy sel'skokhozyaistvennogo proizvodstva Severa* (Agroclimatic Foundations of Agriculture in the North), Leningrad: Gidrometeoizdat, 1982.
- Khokhryakov, A.P., Data on the Flora of Southern Magadan Oblast, in *Flora i rastitel'nost' Magadanskoi oblasti* (Flora and Vegetation of Magadan Oblast), Vladivostok: DVNTS Akad. Nauk SSSR, 1976, pp. 3–36.
- Khomentovskii, P.A., *Ekologiya kedrovogo stlanika (Pinus pumila (Pall.) Regel) na Kamchatke (obshchii obzor)* (The Ecology of Mountain Pine (*Pinus pumila* (Pall.) Regel) in Kamchatka: A General Review), Vladivostok: Dal'nauka, 1995.

- Klyukin, N.K., Climate, in *Sever Dal'nego Vostoka* (The North of the Russian Far East), Moscow: Nauka, 1970, pp. 101–132.
- Kolesnikov, B.P., *Chozeniya (Chosenia macrolepis* (Turcz.) Kom.) *i ee tsenozy na Dal'nem Vostoke (Chosenia macrolepis* (Turcz.) Kom. and Its Cenoses in the Far East), Moscow, 1937.
- Kolesnikov, B.P., Vegetation, in *Dal'nii Vostok* (The Far East), Moscow, 1961, pp. 183–245.
- Kotlyarov, I.I., Mountain Pine Thickets on the Sea of Okhotsk Coast, in *Pochvy i rastitel'nost' merzlotnykh raionov SSSR: Mat-ly V Vsesoyuzn. simpoz.* (Proc. V All-Union Symp. on Soils and Vegetation of Permafrost Regions of the Soviet Union), Magadan, 1973, pp. 208–214.
- Kryuchkov, V.V., On Factors Providing for the Development of Shrublike Tree Forms in the Subarctic, *Vestn. Mosk. Gos. Univ., Ser. 4: Geol.*, 1968, no. 3, pp. 70–80.
- Kryuchkov, V.V., *Chutkaya Subarktika* (The Perceptive Subarctic), Moscow: Nauka, 1976.
- Mazurenko, M.T., *Biomorfologicheskie adaptatsii rastenii Krainego Severa* (Biomorphological Adaptations of Plants in the Far North), Moscow: Nauka, 1986.
- Mazurenko, M.T. and Moskal'yuk, T.A., Specific Ecological Features of *Chosenia arbutifolia* (Pall.) A. Skvorts. (Salicaceae), *Ekologiya*, 1991, no. 2, pp. 13–21.
- Mezhenniy, A.A., Some Features of Morphogenesis and Ecology of Conifers and Their Distribution in Northeastern Asia, in *Biologiya i produktivnost' rastitel'nogo pokrova Severo-Vostoka* (Biology and Productivity of Plant Cover in the Northeast), Vladivostok: DVNTS Akad. Nauk SSSR, 1976, pp. 64–79.
- Molozhnikov, V.N., *Kedrovyy stlanik gornyykh landshaftov Severnogo Pribaikal'ya* (Mountain Pine in Highland Landscapes of the Northern Baikal Region), Moscow: Nauka, 1975.
- Papernov, I.M. and Zamoshch, M.M., Geophysical Features of Adaptation of Pioneer Woody Vegetation in Disturbed Lands of Northeastern Regions, *Biologicheskie problemy Severa: Tez. dokl. X Vsesoyuzn. simpoz.* (Biological Problems in the North: Abstr. X All-Union Symp.), Magadan, 1983, pp. 292–293.
- Savile, D.V.O., *Arctic Adaptation in Plants*, Plant Res. Inst. Monogr., vol. 6, Ottawa, 1972.
- Shamshin, V.A., *Kamennoberezovye lesa Kamchatki: biologiya, ekologiya, stroenie drevostoev* (Mountain Pine Forests in Kamchatka: Biology, Ecology, and Tree Stand Structure), Moscow: GEOS, 1999.
- Shamurin, V.F., Seasonal Rhythm and Ecology of Blossoming in Tundra Plant Communities of Northern Yakutia, in *Prisposoblenie rastenii Arktiki k usloviyam sredy* (Plant Adaptation to Environmental Conditions in the Arctic), Moscow: Nauka, 1966, pp. 5–125.
- Sochava, V.B., Dark Conifer Forests, in *Rastitel'nyi pokrov SSSR* (Plant Cover of the Soviet Union), Moscow: 1956, vol. 1, pp. 132–216.
- Starikov, G.F., *Lesa Magadanskoi oblasti* (Forests of Magadan Oblast), Magadan: Magadan. Knizhn. Izd., 1958.
- Sukachev, V.N. and Zonn, S.V., *Metodicheskie ukazaniya k izucheniyu tipov lesa* (Methodological Guidelines for the Study of Forest Types), Moscow: Akad. Nauk SSSR, 1961.
- Tikhomirov, B.A., *Kedrovyy stlanik, ego biologiya i ispol'zovanie* (Mountain Pine: Biology and Use), Moscow: Akad. Nauk SSSR, 1949.
- Utkin, A.I., Studies on Forest Biogeocenoses, in *Programma i metodika biogeotsenologicheskikh issledovaniy* (The Program and Methods of Biogeocenological Studies), Moscow: Nauka, 1974, pp. 281–317.
- Vasil'ev, V.N., Stone Birch (*Betula ermani* Cham. s.l.): Ecology and Cenology, *Bot. Zh.*, 1941, vol. 26, nos. 2–3, pp. 172–208.
- Zhmylev, P.Yu., Alekseev, Yu.V., Karpukhina, E.A., and Balandin, S.A., *Biomorfologiya rastenii: Illyustrirovannyy slovar'* (Plant Biomorphology: An Illustrated Dictionary), Moscow: Mosk. Gos. Univ., 2002.