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Influence of brushing frequency on birch population structure after felling[1]

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Abstract: Populations of *Betula pendula* and *Betula pubescens* in felling stands subject to different brushing regimes were studied in the southern taiga forest (Tsentralno-Lesnoi Biosphere Zapovednik, Russia). The stands are 14- and 20 y old and are situated in the *Oxalis* type of spruce forest. The number of birch saplings, the height and ontogenetic stage (reflecting the biological age) of individual saplings in the community were determined in ten 5- × 10-m plots, five in a 14-y-old stand that had undergone a single brushing event and five in a 20-y-old stand that had undergone three (regular) cleanings. In the 14-y-old stand, birches were more numerous (the total number of birch saplings was 10,800.0 ± 1365.3 stems·ha^{-1}), saplings were higher (*B. pendula*: 2.59 ± 0.08 m; *B. pubescens*: 1.80 ± 0.12 m), and populations were more mature (most *B. pendula* saplings had changed to tree stage *v* from bush stage *im*). The total number of saplings in the 20-y-old stand was 1120.0 ± 338.2 stems·ha^{-1}, the mean height of *B. pendula* was 2.47 ± 0.45 m, the mean height of *B. pubescens* was 1.45 ± 0.14 m, and saplings in immature stages dominated. Natural forest regeneration was dominated by *B. pendula*, which was almost twice as abundant as *B. pubescens* in the 20-y-old stand, and three times more abundant in the 14-y-old stand.
Keywords: *Betula pendula, Betula pubescens*, birch, brushing, cleaning, clearcuts, ontogenetic stages, spruce plantations.

Résumé : Les populations de *Betula pendula* et de *Betula pubescens* de peuplements forestiers soumis à différents régimes de débroussaillement ont été étudiées dans le sud de la taïga (Tsentralno-Lesnoi Biosphere Zapovednik, Russie). Les peuplements âgés de 14 et de 20 ans étaient situés dans des pessières de type *Oxalis*. Le nombre, la hauteur et le stade ontogénique (reflète l'âge biologique des individus dans une communauté) des gaules de bouleau ont été mesurés dans 10 parcelles (5 × 10 m) ayant subit un seul débroussaillement ou trois dégagements réguliers. Dans le peuplement âgé de 14 ans et ayant subit une seule opération de débroussaillement, les populations de bouleaux étaient plus denses (10 800.0 ± 1365.3 tiges·ha^{-1}), les gaules plus grands (2.59 ± 0.08 m – *B. pendula* et 1.80 ± 0.12 m – *B. pubescens*) et les populations plus matures (la majorité des gaules de *B. pendula* était passée du stade de buisson - *im* à celui d'arbre - *v*). Dans le cas du peuplement âgé de 20 ans et ayant subit un dégagement régulier, la densité des gaules était de 1120.0 ± 338.2 tiges·ha^{-1}, la hauteur moyenne de *B. pendula* de 2.47 ± 0.45 m, et pour *B. pubescens* de 1.45 ± 0.14 m, et les gaules immatures dominaient. La régénération naturelle était dominée par *B. pendula* qui était presque deux fois plus abondant que *B. pubescens* dans le peuplement de 20 ans et trois fois plus abondant dans le peuplement de 14 ans.
Mots-clés : *Betula pendula, Betula pubescens*, bouleau, coupes à blanc, débroussaillement, dégagement, plantations d'épinettes, stades ontogéniques.

Nomenclature: Czerepanov, 1995.

Introduction

Two birch species (*Betula pendula* and *B. pubescens*) tend to dominate clearings in coniferous and mixed forests in Europe (Nikolov & Helmisaari, 1992). Sexual reproduction and vegetative regeneration are both important processes for the invasion, colonization, and maintenance of birches on sites after large disturbances in the boreal forest. The importance of these two means of propagation in the population dynamics of *Betula* species is still unclear.

Regeneration of *Betula* species in cutover stands occurs by sprouting from stumps. The sprouts that arise from the lower parts of stems emanate from dormant buds that grow outward just under the bark (Kauppi, Rinne & Ferm, 1987; Atkinson, 1992). The sprouts typically develop into shoots only after destruction or death of the tree crown. Sprouting capacity depends on the age and size of stumps (Denisov, 1974), season of cutting (Johansson, 1992; Kozlowski, 2002), and light conditions (Melekhov, 1975). Saplings originating from sprouts grow much faster than seed-originated saplings during the first few years (Paukkonen & Kauppi, 1998).

In clearcut areas, birch seed germination and early seedling development are more successful on the disturbed soils of skid roads, tracks, and planting furrows (Borisova *et al.*, 2001; Zhukovskaya, 2002). Mineral soil is generally a good seedbed for *Betula* species because of its high water infiltration capacity, favourable aeration, and good hydraulic contact between soil particles and seeds (Miles, 1973; Raulo & Malkonen, 1976; Karlsson, 1996; Karlsson *et al.*, 1998; Kozlowski, 2002). Seedlings emerge from fresh seeds after several months (Dekatov, 1961; Shimanjuk, 1964). Seedling survival is characterized by a sharp decline in seedling density during the first two growing seasons (Zasada, Sharik & Nygren, 1992).

The role a plant population plays in a community is determined by the plant's structure and abundance, expressed in terms of both the ontogenetic stage and the

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chronological age of the individuals. The main problem for scientists studying the age structure of tree sapling populations is the necessity to uproot all trees in order to ascertain their origins as vegetative or sexual. Another problem is the difficulty of determining the age of seedlings of *Betula* and *Abies* species, among others, as these species often retract part of their stems into the soil (the underground portion of the stem is known as a ksilopodium). It can be difficult to find the root collar in these underground stems. A third problem is that it is not clear how to determine the age of sprouts that have formed on 5- to 10-y-old trees. We conclude that it is fairly difficult to determine the calendar age of birch seedlings and saplings. A classification by ontogenetic stages, on the other hand, is quite feasible (Ulanova, 2000). Ontogenetic stages mark the biological or functional age of plants. Individual plants of different ontogenetic stages may play different roles in a plant community (Rabotnov, 1978; 1985). Ontogenetic stage has greater significance than calendar age in analyzing the structure and dynamics of populations (Gatsuk *et al.,* 1980). The spectrum of ontogenetic stages found in a cutover will indicate the pathways of reforestation under way.

We use the Russian classification of ontogenetic stages according to Rabotnov (1978; 1985). In this classification, the ontogeny of plants can be divided into stages based on the origin of individuals (seed or vegetative) and on certain juvenile and adult characteristics.

The first aim of our investigation was to test for differences in *B. pendula* and *B. pubescens* populations formed in 14- and 20-y-old stands after brushing operations of different frequency. The second aim was to compare the population structure of *B. pendula* and *B. pubescens* using such characteristics as numbers, heights, and ontogenetic stages in stands 14 and 20 y after felling.

Methods

STUDY SITE

The investigations were carried out in the East European taiga (southern taiga zone) situated in the Tver Region of Russia, in the Tsentralno-Lesnoi Biosphere Zapovednik (56° 26'–39' N, 32° 39'–33° 01' E). This area is in the centre of the Russian Plain, in the southwest part of the Valday Uplands at the watershed of the Volga and Western Dvina rivers (Karpov, 1973). The general climate in the reserve is moderate continental, with an average temperature of 3.6 °C. The surficial geology consists of quaternary loamy sediments covering Devonian limestone. The total area of the Zapovednik is 24,447 ha, and its surrounding buffer zone is 46,061 ha.

The Zapovednik territory is a continuous forest expanse stretching 19 km north to south, and 17 km from west to east. The Zapovednik is 94% forested, with spruce forests dominating (47%). Pine forests (10%), represented by bog communities, and black alder forests (1–2%), located in river and stream valleys, are also indigenous. Secondary deciduous forests make up approximately 40% of the total forest area. These secondary stands have developed from windfalls, fires, and cuttings that took place during the closure of the Zapovednik.

The study sites are located in the buffer zone of the Zapovednik, in a region of 100- to 120-y-old pristine spruce–*Oxalis* forest. The two sites are located in equivalent habitats about 800 m from each other. The mature forest in the study area is dominated by *Picea abies*, with *Betula pendula* and occasional *Populus tremula.* Both study sites are situated on the largest clear cut area with dominant understory of *Calamagrostis epigeios. Calamagrostis epigeios* is a dominant plant that appears in clearcuts in the first year after cutting. This species can establish by seed or from long horizontal rhizomes; it disappears after the tree canopy closes (Ulanova, 2000).

Experimental sample plots were located in sites that were logged 14 and 20 y earlier. Felling was conducted with full removal of wood and shrubs. Tree saplings (natural regeneration) were fully removed during felling. Each cutblock, nearly 10 ha in size, was logged in the spring. Mechanical harvesters and skidding tractors were used for timber cutting and removal, slash piled in rows 10–11 m from each other. In May of the second year after logging, 3-y-old bare-root spruce seedlings were planted in the berm of furrows at a density of 8000 stems·ha^{-1}.

Different cleaning strategies were used in the sample plots after planting the spruce. A single cleaning 7 y after logging was used in the 14-y-old site. Birch saplings were removed between the rows of spruce planting. Stand cleaning was carried out using manual cutting at a height of about 30 cm from the ground in both sites. The 20-y-old site experienced cleanings at 5, 8, and 13 y after logging, with all birch saplings removed.

EXPERIMENTAL DESIGN

In each stand, five 5- × 10-m plots located along a transect running perpendicular to the rows of spruce saplings were used to sample birch populations (Figure 1). Plots were located every 6 m and included rows of planted spruce saplings in the middle of the sample plot and two segments of inter-row spacing between the planted rows of spruce.

All trees (planted spruce saplings and all those resulting from natural regeneration) found in each plot were counted and measured. In each plot we recorded the number, height, and ontogenetic stage of birch saplings and the number and height of spruce stems.

Ontogenetic stages of birch saplings were determined using the scale developed by Chistyakova (1989), Smirmova *et al.* (1999) and Gatsuk *et al.* (1980). We differentiated stages according to the following description (Figure 2):

- Seedlings (*pl*) have two cotyledons and 2–6 simple leaves with denticulate margins.
- Juvenile (*j*) plants have an unbranched monopodial shoot, with widely ovate, slightly hairy leaves without cotyledons. Shoots of sprouts start to develop from the *juvenile* ontogenetic stage and develop into the *immature* stage quickly. Shoots that have not lignified usually die after the first autumn frosts.
- Immature (*im*) stages are characterized by the beginning of shoot branching. At this stage, the shoot system has branches of a low order, but a definite crown has not yet formed. Leaves are widely ovate and downy, with biser-

rate edges and visible glandular hairs. This ontogenetic stage is divided into two subgroups: *im1*, with second- and third-order branches and an overall height of the shoot system approximately equal to its diameter, and *im2*, with third- and fourth-order branches and an overall height to diameter ratio of 3:2.

- Virginile (*v*) plants are small, fast-growing sympodial branching trees with a clearly defined trunk and branched crown. Leaves have an ovate or rhomboid form. A tree in this stage has not yet flowered. In this stage we distinguish two subgroups: *v1* trees have a grey trunk with pink colour and a broad pyramidal crown with fourth- and fifth-order branches and *v2* trees have a white trunk and a narrow pyramidal crown with fifth- and sixth-order branches.

Differences between the heights of plants at different ontogenetic stages were tested by *t*-tests.

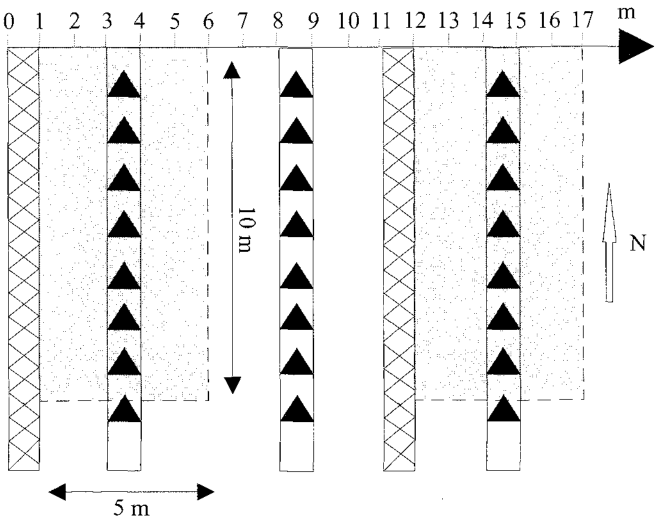

FIGURE 1. Schematic picture of sampling strategy in 14- and 20-y-old sites after felling. Sample plots (5 × 10 m) are situated along a transect running perpendicular to rows of spruce plantings. Triangles : spruce plantings, crosses: row of slash.

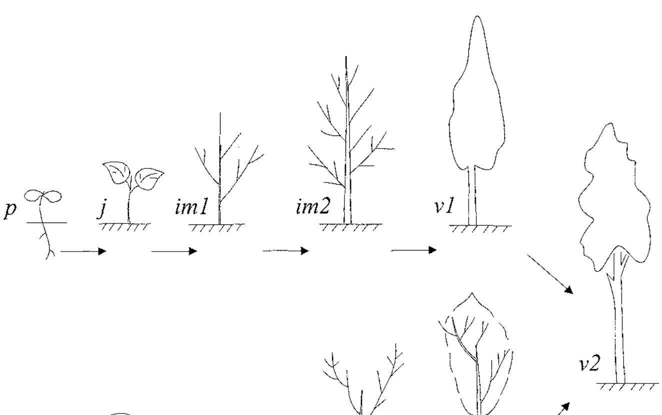

FIGURE 2. Ontogenetic stages of *Betula pendula* seedlings and sprouts. Arrows represent seedling stages and arrows with × represent sprout stages.

Results

In the 14-y-old, once-cleaned stand, birch saplings formed a closed canopy. The density recorded for *B. pendula* was 8080.0 ± 2343.0 stems·ha^{-1} (mean ± SD), and the density for *B. pubescens* was 2720.0 ± 1136.7 stems·ha^{-1} (Table I). A large portion of the forest regeneration of this area consisted of aspen suckers (5480.0 ± 3861.6 stems·ha^{-1}). The number of surviving saplings of *Picea abies* was 3640.0 ± 1134.9 stems·ha^{-1}. The majority of spruce saplings ranged from 1.5 to 3 m in height (2.45 ± 0.09 m; mean ± SE); all spruce saplings were located in or under a birch and aspen canopy. *Salix caprea* occurred at a density of 3480.0 ± 1847.2 stems·ha^{-1}.

In the 20-y-old stand, canopy closure had occurred in the rows of planted spruce saplings, but not in between rows. The total density of spruce saplings was 5240.0 ± 684.1 stems·ha^{-1} (Table I). These saplings formed a canopy at a height of 6–7 m (5.79 ± 0.18; mean ± SE). Birch was the dominant species of natural regeneration. The density of surviving saplings (after the series of repeated cleanings) was 720.0 ± 609.9 stems·ha^{-1} for *B. pendula* and 400.0 ± 244.9 stems·ha^{-1} for *B. pubescens*. Other trees species present in high numbers included *Alnus incana*, *Salix caprea*, and *S. myrsinifolia*.

STRUCTURE OF BIRCH POPULATIONS IN THE 14-Y-OLD STAND

Betula pendula regeneration dominated this once-cleaned cutblock. The density of *B. pendula* saplings totalled 202 stems·250 m^{-2}, or 8080 stems·ha^{-1}.

Most of the *B. pendula* saplings were first-generation sprouts that had appeared on the stems of saplings after the single cleaning. Birch stems were distributed evenly within the sample plots. The majority of *B. pendula* stems were 1 to 4 m tall (2.59 ± 0.08 m; mean ± SE), with occasional trees 5–7 m tall (Figure 3a). These saplings had established by seed and had survived by sprouting after the single cleaning operation several years before.

The population structure of *B. pendula* was characteristic of an invasive population, consisting of trees of different young ontogenetic stages: juvenile (*j*), immature (*im1*, *im2*),

TABLE I. Density (stems·ha^{-1} ± SD) of regenerating tree species and planted spruce saplings observed in felling stands with different brushing frequencies.

Tree species	14-y-old stand (single cleaning) (Mean ± SD)	20-y-old stand (repeated cleanings) (Mean ± SD)
Betula pendula	8080.0 ± 2343.0	720.0 ± 609.9
Betula pubescens	2720.0 ± 1136.7	400.0 ± 244.9
Populus tremula	5480.0 ± 3861.6	360.0 ± 589.9
Picea abies (planted)	3640.0 ± 1134.9	5240.0 ± 684.1
Salix caprea	3480.0 ± 1847.2	1800.0 ± 969.5
Salix myrsinifolia	2280.0 ± 794.9	640.0 ± 1322.1
Sorbus aucuparia	1120.0 ± 1196.7	400.0 ± 583.1
Salix aurita	880.0 ± 540.4	80.0 ± 109.5
Alnus incana	360.0 ± 804.9	840.0 ± 841.4
Salix pentandra	360.0 ± 357.8	280.0 ± 521.5
Salix cinerea	320.0 ± 303.3	-
Salix starkeana	200.0 ± 346.4	-
Acer platanoides	-	80.0 ± 109.5
Tilia cordata	-	80.0 ± 178.9
Total	28,920	10,920

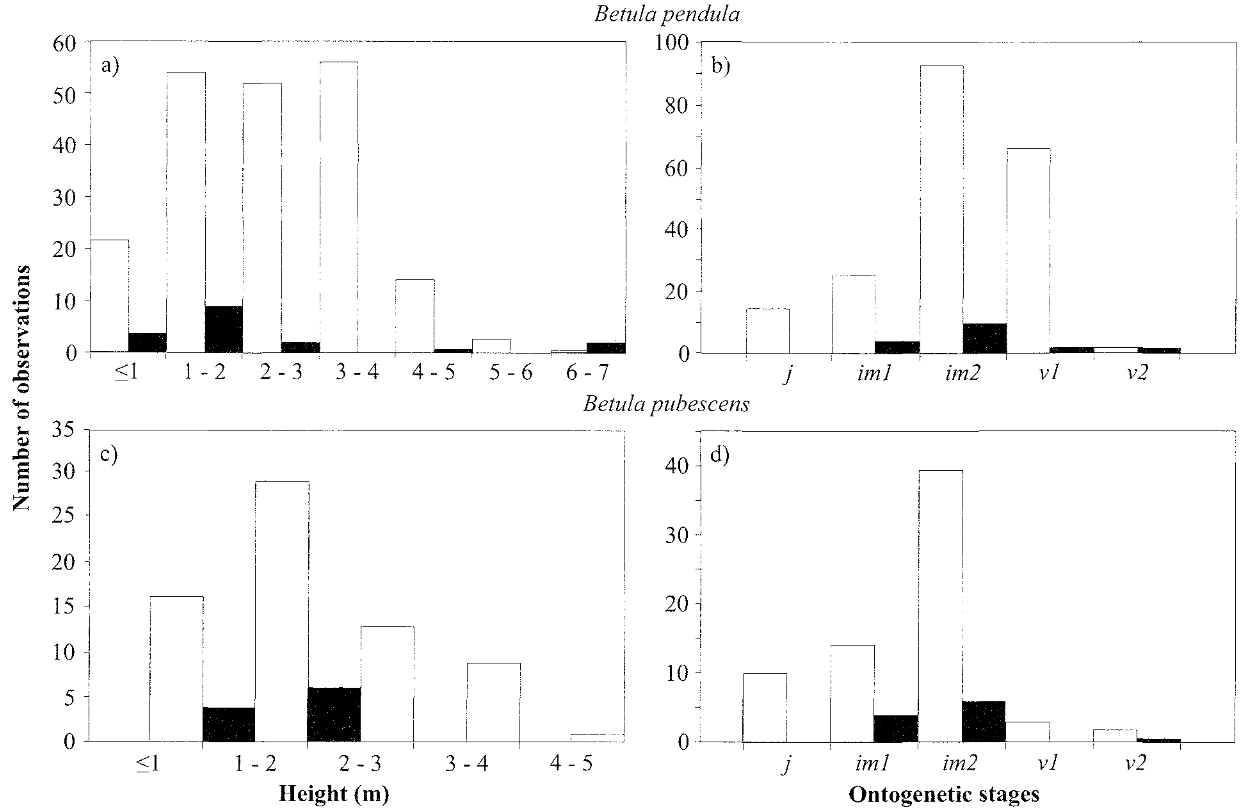

FIGURE 3. Population structure of *Betula pendula* and *B. pubescens* in felling stands with different brushing frequencies. White bars: 14-y-old stand with one cleaning; black bars: 20-y-old stand with regular cleaning.

and virginile (*v1*, *v2*) stages (Table II). There was no soil and herb layer disturbance, so birch seedlings (*pl*) were absent. Trees in the *im2* stage dominated (93 stems·250 m^{-2}, or 3720 stems·ha^{-1}) (Figure 3b). These saplings had a branching shoot system. Large numbers of saplings were already at the next stage, *v1* (66 stems·250 m^{-2}, or 2640 stems·ha^{-1}). Trees at the *v1* stage were 2.5–5.2 m in height, with clear differentiation of the branch system and slender crowns. The saplings in the *j* stage (15 stems·250 m^{-2}, or 600 stems·ha^{-1}) were second-generation sprouts, which appeared on the stems of sprouts after the cleaning operation.

Saplings of *B. pubescens* were also found as first generation sprouts. *Betula pubescens* stems were distributed evenly in the sample plots. The overall density of *B. pubescens* saplings in the 14-y-old stand was 68 stems·250 m^{-2}, or 2720 stems·ha^{-1}. Most of the *B. pubescens* stems were 1–2 m (1.80 ± 0.12 m; mean ± SE) in height (Figure 3c) and grew under the canopy of *B. pendula*. We found one birch in the 4-m height class that had survived the early cleaning.

The structure of the *Betula pubescens* population was also of the invasive type (Table III). The spectrum of ontogenetic stages consisted of all young stages from *juvenile* to *virginile*. Saplings in the *im2* stage were the most prevalent (39 stems·250 m^{-2}, or 1560 stems·ha^{-1}). Saplings of *B. pubescens* in this stage were 1.1–3.3 m in height. The second most prevalent stage was the previous *im1* stage (14 stems·250 m^{-2}, or 560 stems·ha^{-1}). Saplings in this stage were characterized by small branches, usually starting at a height of 0.4–1.5 m. These saplings were found mainly in the herbaceous layer or lower shrub layer. Only a few scattered trees attained the *virginile* (*v1*) stage (3 stems·250 m^{-2}, or 120 stems·ha^{-1}), and two saplings (80 stems·ha^{-1}) that had established from seed were found in the *v2* stage, the last stage before reproduction.

STRUCTURE OF BIRCH POPULATIONS IN THE 20-Y-OLD STAND

Only 18 stems·250 m^{-2} (720 stems·ha^{-1}) of *B. pendula* survived after a series of early cleanings in this stand (Table II).

Most of the saplings were sprouts of *B. pendula*. These were generally second- and third- generation sprouts, which means that they formed on the stems of sprouts after the first and second cleaning operations. All birches were growing in the rows of planted spruce.

The mean height of saplings was 2.47 ± 0.45 m (mean ± SE). Two size classes of *B. pendula* saplings prevailed in the 20-y-old stand: those < 3 m in height and those between 5 and 7 m in height. (Figure 3a). Saplings 1–2 m tall were dominant. This population of *B. pendula* was of the young invasive type, consisting of plants in the *immature* and *virginile* stages (Table II). The saplings in this category generally lacked trunk and crown differentiation. Trees in the *im2* stage occurred most often (10 stems·250 m^{-2}, or 400 stems·ha^{-1}). Only four saplings (160 stems·ha^{-1}) were found in *virginile* stages.

After the series of early cleanings, the number of *B. pubescens* saplings was 10 stems·250 m^{-2}, or 400 stems·ha^{-1} (Table III). All saplings were second- and third-generation sprouts and were found both in the rows of planted spruce and in the inter-row spaces. The height of those saplings ranged from 1 to 2 m (1.45 ± 0.14; mean ± SE) (Figure 3c).

TABLE II. Heights and ontogenetic stages of *Betula pendula* saplings in 14- and 20-y-old felling stands.

	H (m) Mean ± SE	H (m) min	H (m) max	Variance	n*	%
14-Y-OLD STANDS						
j	0.53 ± 0.07	0.1	1.0	0.078	15	7
im1	1.25 ± 0.06	0.5	1.5	0.080	26	13
im2	2.36 ± 0.05	1.6	3.5	0.271	93	46
v1	3.79 ± 0.06	2.5	5.2	0.263	66	33
v2	6.50 ± 0.50	6.0	7.0	0.500	2	1
20-Y-OLD STANDS						
j	-	-	-	-	-	-
im1	0.87 ± 0.12	0.5	1.0	0.062	4	22
im2	2.00 ± 0.15	1.5	3.0	0.222	10	56
v1	3.50 ± 1.50	2.0	5.0	4.500	2	11
v2	7 ± 0	7.0	7.0	0.000	2	11

* Number of saplings on studded 250 m^2.

TABLE III. Heights and ontogenetic stages of *Betula pubescens* saplings in 14- and 20-y-old felling stands.

	H (m) Mean ± SE	H (m) min	H (m) max	Variance	n*	%
14-Y-OLD STANDS						
j	0.23 ± 0.03	0.15	0.4	0.008	10	15
im1	1.11 ± 0.11	0.4	1.5	0.172	14	21
im2	2.18 ± 0.09	1.1	3.3	0.303	39	57
v1	3.66 ± 0.07	3.6	3.8	0.013	3	4
v2	4.05 ± 0.15	3.9	4.2	0.045	2	3
20-Y-OLD STANDS						
j	-	-	-	-	-	-
im1	1 ± 0	1.0	1.0	0.000	4	40
im2	1.75 ± 0.11	1.5	2.0	0.075	6	60

* Number of saplings on studded 250 m^2.

The population structure of the species lacked the full spectrum of stages and hence is interpreted as invasive, with only the *immature* stages present (Table III) and with the *im2* stage prevalent (60% of stems).

Discussion

Saplings of different ontogenetic stages have specific growth and morphological characteristics and show definite structural-functional stages (Gatsuk *et al.*, 1980). Each stage has fixed size parameters. Each of the studied *B. pendula* and *B. pubescens* stages is significantly different in height from the other stages of that species ($P < 0.01$; t-test). Sprouts of *Betula* dominate in both sampling areas and start their development from the *juvenile* stage, characterized by one monopodial shoot with a height of 0.1 to 1 m. The variance in height of *juvenile B. pendula* and *B. pubescens* saplings is 0.078 and 0.008, respectively (Tables II and III). Investigation of the saplings variances in different ontogenetic stages showed bigger variances of height in older stages for both species. *B. pendula* saplings in the *v1* stage are trees with a clearly defined trunk (from 2.5 to 5.2 m tall) and a branched crown; saplings in this stage have the biggest variance of height for this species: 0.263 in the 14-y-old stand. *Betula pubescens* sprouts in the *im2* stage (from 1.1 to 3.3 m tall) have the biggest variance of height for their species: 0.303, in the 14-y-old stand.

Our previous investigations (Zhukovskaya & Ulanova, 2004; Ulanova *et al.*, 2005) showed that by the second year seedlings of *Betula* attain the *j* stages (sprouts start their development from this stage) and that by the first 3–4 y, birch saplings grow to the *im1* stage and stay in the herbaceous layer. The main competitor of birch seedlings at this stage (*im1*) is *Calamagrostis epigeios*. At this stage of succession, interspecific competition stimulates the attrition of some seedlings. In 5–6 y the naturally regenerated birch saplings form a closed canopy in clearcuts. In this young birch forest stage, intraspecific competition for light and mineral nutrition between birches in the *im2* ontogenetic stage plays the main role. Most depressed, weaker trees perish if they do not reach the *im2* ontogenetic stage within 5–6 y.

Range of height for tree saplings would be better to analyse with determination of ontogenetic stages. The range of heights in the plant population increases with the age of the plants as a result of increasing competition. Trees of equal height can be in different ontogenetic stages and have different future trends of development. Studying only the range of heights will not show the biological role of individual saplings in the community or provide sufficient information to forecast development of the population as a whole. Analysis of ontogenetic stages is a more appropriate and informative method, reflecting definite size parameters and the functional position of individual saplings in the plant community and enabling forecasts of the development of the population.

The structure of birch populations differed in stands with different brushing frequencies. There were 2.8 times as many birch saplings in the 14-y-old stand with the single brushing treatment as in the 20-y-old stand that had been brushed three times at intervals of 3–5 y. Every new brushing treatment appeared to increase the mortality of the weakest members of each birch species.

Repeated brushing reduced the height of saplings in the stand. Most *B. pendula* stems in the 20-y-old stand attained a height of only 1–2 m. In the 14-y-old stand, the stems achieved a height of 3–4 m (Figure 3a). Most *B. pubescens* stems in the 20-y-old stand were less than 2 m in height, but in the 14-y-old stand most trunks achieved heights of 3 to 4 m (Figure 3c).

The cleaning operations decreased the number and height of birch stems in the stand and as a result changed the ontogenetic structure of these populations. Regular cleaning promoted rejuvenation of the birch population by destroying the saplings from the oldest ontogenetic stages and encouraging the growth of saplings (sprouts) at younger stages.

According to the ontogenetic structure of the birch populations in the 20-y-old stand, those populations were "younger" than the populations found in the 14-y-old stand. In the 20-y-old stand, *immature* saplings of *B. pendula* (without well-formed crowns and with second- and fourth-order branching shoot systems) predominated. In contrast, in the 14-y-old stand, a large proportion of the population was made up of young *virginile* saplings with well-formed crowns and fourth- and fifth-order branches (Figure 3b). Saplings of *B. pubescens* attained *virginile* stages only in this stand (Figure 3d).

In naturally regenerated populations, all saplings ought to attain 4–5 m in height after 14 y of growth and should have formed a slender (narrow) pyramidal crown (*v1–v2* stages). After 20 y of growth, birch saplings would normally attain generative (reproductive) stages (Chistyakova, 1989).

The brushing caused weakening of birch saplings in the cutting stand and changed their position in the community from overstory to understory. Not only did the number of saplings decrease and individuals returned to younger ontogenetic stages, but also the vitality of saplings decreased as a whole. Carbohydrate reserves undoubtedly decreased after stem cutting, leading to the death of some roots. This, in turn promoted the formation of saplings with retarded growth and development (Kudryavcev, 1953; Ribalchenko, 1983). We found that the range of heights of plants at different ontogenetic stages was more restricted and that saplings in the same stages were shorter in the stand with regular cleaning for both species (Tables II and III). Thus, *im1* saplings of *B. pendula* grew up to 1.5 m in the stand with a single cleaning and up to 1 m in the regular cleaning stand, and saplings in the next stage, *im2,* had a height between 1.6 and 3.5 m in the first case and between 1.5 and 3 m in the second. The statistical analyses showed that the *im2* saplings in the 20-y-old stand were significantly shorter than saplings at this stage in the 14-y-old stand ($P < 0.05$; *t*-test). Thus, *virginile* saplings of *B. pendula* were taller in the 14-y-old stand with one brushing operation than in the 20-y-old stand with regular brushing (Tables II and III).

Though only *B. pendula* grew in the mature forest before logging, after clearcutting we observed natural regeneration by both birch species at both study sites. Regeneration by *B. pendula* predominated, being twice as abundant as *B. pubescens* in the 20-y-old stand and three times more abundant than *B. pubescens* in the 14-y-old cutting stand. Denisov (1979) suggests that regeneration by both birch species occurs independently of ecological conditions in the first years after logging, but that only one species subsequently dominates the stand, determined by site conditions. *Betula pubescens* has generally been observed to dominate more humid sites than those occupied by *B. pendula* in mature forests (Denisov, 1979).

The population structure of *B. pendula* and *B. pubescens* differs between the study stands. The mean heights of *B. pendula* and *B. pubescens* were 2.59 ± 0.08 m and 1.80 ± 0.12 m, respectively, in the 14-y-old cutting stand and 2.47 ± 0.45 m and 1.45 ± 0.14 m, respectively, in the 20-y-old stand. The mean heights of *B. pendula* and *B. pubescens* saplings in the same ontogenetic stages are different. Thus, in the 14-y-old stand, the youngest *juvenile* sprouts of *B. pendula* and *B. pubescens* were 0.53 ± 0.07 m in height and 0.23 ± 0.03 m in height, respectively, and the oldest (*v2*) sprouts were 6.50 ± 0.50 m and 4.05 ± 0.15 m in height, respectively (Tables II and III). However, significant differences were found only in the j stages, ($P < 0.01$, *t*-test). The distribution of saplings in the different ontogenetic stages for both species in equal conditions (brushing frequency) differ. Therefore, in the 14-y-old stand with a single cleaning, the *B. pendula* saplings in the *im2* and *v1* ontogenetic stages and the *B. pubescens* saplings in the *im* stages prevailed. Moreover, in the 20-y-old stand with regular cleaning *B. pendula* had the oldest stages of saplings.

Conclusion

The structures of birch populations between cutting stands with different brushing frequency. Regular brushing not only reduces the density and mean height of birch saplings, but also weakens them by reducing their vitality. It also leads to rejuvenation of the birch population by destroying the saplings from the oldest ontogenetic stages and encouraging the growth of sprouts at younger stages. The two birch species contribute to the natural reforestation of felling stands with different brushing frequency in *Oxalis* type of spruce forest. However, *B. pendula* saplings dominate in terms of density and height. The population of *B. pendula* as a whole is more mature and better suited to these habitats.

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