Chapter 5
Recovery of Forest Vegetation After Fire Disturbance

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5.1 Introduction

Fire is the dominant form of disturbance in boreal forests (Wein and MacLean 1983; Van Cleve et al. 1986; Payette 1992; Rees and Juday 2002). In the Siberian cryolithic zone, ground fires are predominant among the disturbance factors; about 1.5% of the total forested area is damaged annually by wild fires (Sofronov et al. 1998). Fire frequency of northern taiga forests varies between once every 20–200 years, with a mean frequency at about once every 80 years (Sofronov and Volokitina 1996; Abaimov et al. 2000). Understanding patterns of development in forest associations is important, because the fires not only transform forest environment such as microclimate condition, temperature and moisture of upper soil layers, and chemical properties of the soils, but also change cycling of mineral nutrients, soil respiration rate, species composition and other biological characteristics of the ecosystem (Schulze et al. 1995; Abaimov et al. 1996, 1997b, 1998; Matsuura and Abaimov 1998; Bourgeau-Chavez et al. 2000; Prokushkin et al. 2000; Shvidenko and Nilsson 2000; Zyryanova et al. 2002, 2004, 2006, 2007). Under extreme climatic conditions, fires can dramatically change directions of development in forest formation and the rate of progressive succession (Abaimov et al. 2000; Abaimov 2005).

The vegetation development following ground fires varies depending on the intensity and history of disturbance, dispersal and germination traits of regenerating species, specific site characteristics, and microtopography. Permafrost and dynamic processes of annual freeze–thaw cycles result in various surface features. Most common are the earth hummock topography and sorted and nonsorted stripes (Bliss 2000; Ershov 2004). The earth hummocks may be 10–50 cm in height and 1–2 m in diameter. Such hummocks occur at level ground or at gentle slopes (1–3°) (Fig. 5.1a; see also Chap. 16, this Vol.). Elongated stripes are common on slopes >3–5° (Fig. 5.1b). The distance between the stripes may vary from 1 m up to 10 m.

Cryogenic microtopography of boreal forests is responsible for patterned hydrothermal and edaphic conditions of forest habitats, as well as for distribution of plants, spatial differentiation of ground vegetation, and its postfire changes in northernmost Siberia (Shcherbakov 1979; Abaimov et al. 1996, 1997a, b, 1998;

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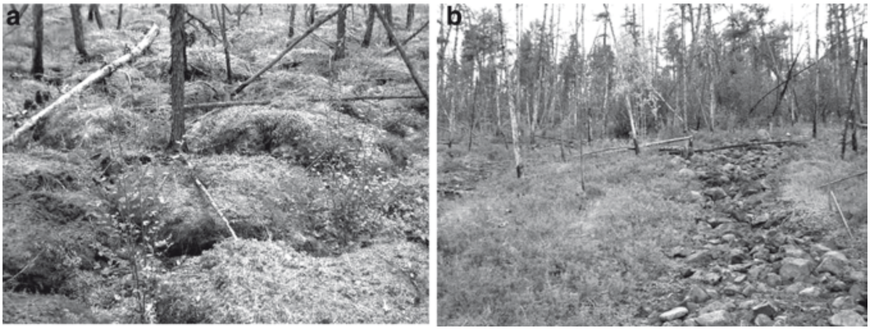

Fig. 5.1 Forest sites with microtopography. (**a**) *Larix gmelinii – Vaccinium vitis-idaea + Vaccinium uliginosum – Hylocomium splendens + Pleurozium schreberi + Peltigera* spp. + *Cladina* spp. association (spot hummock-depression microrelief). (**b**) *Larix gmelinii – Ledum palustre + Vaccinium uliginosum – Aulacomnium turgidum + Pleurozium schreberi* association (elongated stripe-depression microrelief) (Photo: O. Zyryanova)

Prokushkin et al. 2000; Zyryanova 2004; Zyryanova et al. 2002, 2007). In this chapter we synthesize the results of previous studies and unpublished data, and discuss influence of microtopographical conditions (microrelief) on recovery of forest vegetation after fire disturbances.

5.2 Approaches to Study Vegetation Recovery

We have investigated associations of *Larix gmelinii* (Rupr.) Rupr. and plant communities developing after major fires in *L. gmelinii*-dominated forests at Tura Experimental Forest, Central Siberia (Table 5.1; see also Fig. 1.3). A series of chronosequence plots were used for estimating the patterns of vegetation development that would occur over some 90 years.

Plant species diversity (the number of species) was determined in sample plots of 100 m^2 in old larch associations and in recently burned areas. Six plots were established in stands developing after forest fires. Plots 1 and 2 were in areas burned in 1994: the former was in Site 2 and the latter was at ca. 30 km east-southeast of Tura along the Nizhnyaya Tunguska River. Plot 3 was located at ca. 50 km north of Tura, and along the Tembenchi River. Plots 4 and 5 were at Site 1 and Site 3 near Tura, respectively. Plot 6 was on the left bank of the Kochechum River at a few kilometers north of Tura. See Fig. 1.3 (Chap. 1) for locations of these study stands, except for plot 3.

Vegetation was described by noting vascular plants, mosses, and lichens, including description of species abundance (percentage cover). Specific similarity (i.e., similarity of floristic composition) between different stages of progressive succession has been compared with Stogren–Radulescu coefficient ρ_{sr} (Schmidt 1984; Degteva 2005).

Table 5.1 Characteristics of the permanent plots used for description of structure in plant associations

Number of plot	Plant association, its geographical location and topography	Year and fire intensity
Sites with complex microtopography		
1	*Larix gmelinii* – *Vaccinium vitis-idaea* + *Vaccinium uliginosum* – green mosses+lichens 64° 19′ N 100° 13′ E Surface of structural step of east-facing slope of plateau, of 1–3° steepness, spot hummock-depression microrelief	1994 Steady ground, middle
2	*Larix gmelinii* – *Duschekia fruticosa*–*Ledum palustre* + *Vaccinium uliginosum* – lichens+green mosses 64° 10′ N 100°44′ E North-facing slope of plateau, of 10° steepness, elongated stripe-depression microrelief	1994 Running ground
3	*Larix gmelinii* – *Betula nana*+*Salix* sp. – *Ledum palustre* + *Vaccinium uliginosum* – lichens+green mosses 64° 48′ N 99°29′ E Down part of south-eastern-facing slope of plateau, of 1–2° steepness, small hillocky microrelief	1990 Strong running ground
Sites without microtopography		
4	*Larix gmelinii* – *Duschekia fruticosa*–*Ledum palustre* +*Vaccinium vitis-idaea* – green mosses 64° 19′ N 100° 14′ E Upper part of west-facing slope of plateau, of 7–9° steepness	1990 Strong running ground
5	*Larix gmelinii* – *Duschekia fruticosa*–*Ledum palustre* +*Vaccinium vitis-idaea* – green mosses 64° 23′ N 100° 12′ E Middle part of east-facing slope of plateau, of 10–12° steepness	1978 Strong running ground
6	*Larix gmelinii* – *Duschekia fruticosa*–*Ledum palustre* +*Vaccinium vitis-idaea* – green mosses 64° 18′ N 100° 14′ E Middle part of west-facing slope of plateau, of 8–10° steepness	1950 Strong running ground after winter selective cutting

To detect the key points and define key plant associations of the postfire forest regeneration, we compared the patterns of experimental species distribution (used in the sense of "observed" distribution throughout this chapter) with standard geometric series and MacArthur models by calculating Shannon's diversity index for each community at a given time (Zyryanova et al. 2004, 2006; see Chap. 2). Also see definitions of the models applied for description of the same approach (Whittaker 1975; Magurran 1988).

Nomenclature of Latin names for plant species follows Czerepanov (1985).

5.3 Patterns of Vegetation Development After Fire

5.3.1 Sites with Complex Microtopography

Conditions of various microtopography result in different burning characteristics during forest fires, and consequently affect the restoration of larch trees and ground vegetation. Under conditions of microrelief characterized by the spot hummock-depressions (meaning hummock-trough topography of small scale as in spots) (plot 1; Table 5.1), a steady ground fire of medium intensity destroyed, first of all, vegetation of the microdepressions. This was caused by a large amount of organic matter accumulated at the bottom of the depressions, which acted as fuel for burning. Dominance of such plants as *Ledum palustre* and *Vaccinium uliginosum* is also responsible for the extensive burning, because these are some of the most fire-prone species in the cryolithic zone (Kurbatski 1970; Shcherbakov 1979). Here, the height difference between the top of the hummock and the bottom of the depression is about 40–50 cm.

The vegetation at the top of the hummocks was preserved in part at least 1 year after the fire, until microtopography began to change: experimental (= observed) distribution is more similar to the geometric series model than to the model of MacArthur (Fig. 5.2). Total number of species decreased 2.5-fold as compared to that of unburned association (Fig. 5.3).

During the following 2 years, soil thermal melioration begins to destroy the microrelief of the site. Also, hydrological and thermal regimes change considerably (Abaimov et al. 2001). By the fourth year after the fire, ground vegetation develops into a secondary grass-moss association dominated by *Calamagrostis lapponica*, *Chamaerion angustifolium*, *Marchantia polymorpha,* and *Ceratodon purpureus* (Zyryanova et al. 2002, 2008). The coincidence of Shannon's indices for experimental and geometric series distributions (Fig. 5.2) suggested that the plant community was formed as a result of interspecific competition (Zyryanova et al. 2002; Zyryanova 2004; see also Whittaker 1975).

Young larch trees were abundant in the burned area: the number of seedlings amounted to 558.5 thousand per hectare (Abaimov et al. 2000). Within 3 years after fire, the number of vascular plants in the burned area became 83% of that of a mature plant community. Plant species composition of the ground vegetation nearly recovered to the prefire level of plant diversity at the fifth year after fire. The total number of species was 1.2–1.3 times larger than that of the unburned association by the eighth and ninth year after fire (Fig. 5.3). Similarity coefficient $\rho_{sr} = -0.08$ detected this pattern owing to the restored prefire species such as *Duschekia fruticosa*, *Empetrum nigrum*, *Juniperus sibirica*, *Tomenthypnum nitens*, etc. (Zyryanova et al. 2002, 2007). New species (*Atragene sibirica*, *Galium boreale*, *Potentilla inquinans*, etc.) also invaded free ecological niches: nonuniformity of experimental distribution was still significant during this period (Fig. 5.2). In 11 years after fire, the larch regrowth formed dense groups of 45% cover. *Arctous erythrocarpa* and *Vaccinium vitis-idaea* restored their dominating positions among dwarf-shrubs,

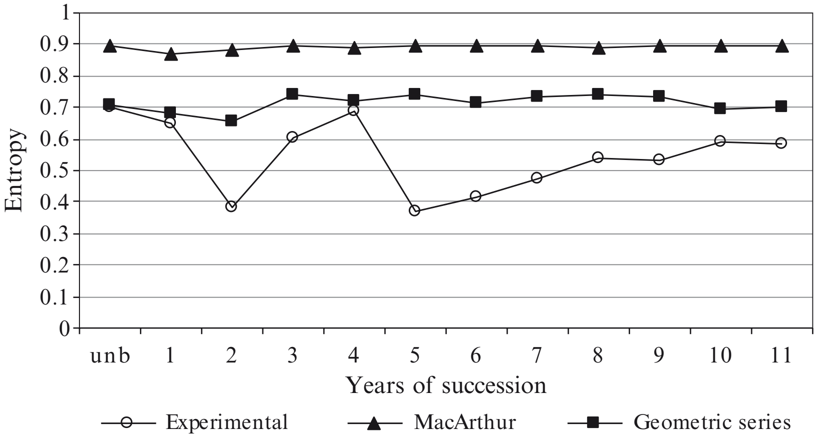

Fig. 5.2 Values of the diversity index expressed as entropy in MacArthur, geometric series, and experimental (= observed) distributions. The diversity indices are scaled with their maximum values for mature larch (unburned) and postfire plant associations at a forest site with spot hummock-depression microtopography (plot 1)

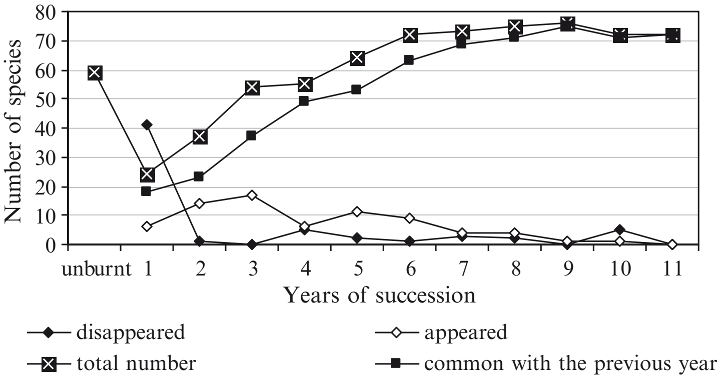

Fig. 5.3 Plant species dynamics at the initial stages of the postfire progressive succession in the forest site with spot hummock-depression microtopography. Total number of species, numbers of disappeared and appeared, as well as common species in relation to the plants of the previous year are shown for each year

while *Ceratodon purpureus*, *Aulacomnium turgidum,* and *Polytrichum uniperinum* dominated the moss cover. Thus, invasion of new species at the sites with spot hummock-depression microtopography lasted for 9 years after steady ground fire of medium intensity. Later on, total number of species showed a tendency of gradual decrease (Fig. 5.3).

Elongated stripe-depression microrelief (plot 2 Tunguska; Table 5.1) produces striped patterns of burning and subsequent regeneration in the ground vegetation (Zyryanova et al. 2002, 2007). Four years after a running ground fire, all main

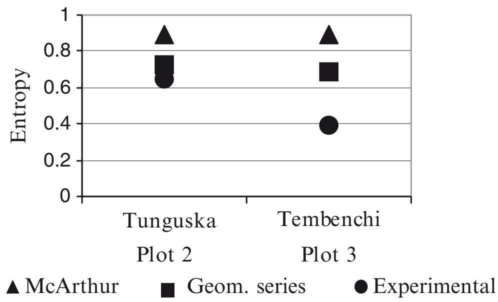

Fig. 5.4 Values of the diversity index expressed as entropy in MacArthur, geometric series, and experimental (= observed) distributions. The diversity indices are scaled with their maximum values for postfire plant associations at a forest site with elongated stripe-depression microtopography (plot 2) in 4 years after fire, and at a forest site with small hillocky microtopography (plot 3) in 8 years after the fire

dominant species (*Vaccinium uliginosum*, *Ledum palustre*, *Hylocomium splendens*) of the understory and ground vegetation were restored from the preserved refugia of these species along the linear depressions. At this year, the experimental distribution was more similar to the geometric series model (Tunguska; Fig. 5.4), suggesting that the species present in the depressions were not damaged by the fire. In contrast, the stripes, convex parts of the ecosystem, were strongly damaged by the running fire and covered by the patches of *Vaccinium vitis-idaea*, *Equisetum scirpoides*, *Rubus arcticus*, *Dryopteris fragrans*, etc. The restoration of the ground floor was not uniform and its rate was rather low.

On the other hand, small hillocky microrelief (the difference between the top of the hillock and the bottom of the depression was about 15–20 cm, plot 3 Tembenchi; Table 5.1) led to total destruction of the ground vegetation by strong running fires, while larch trees were only weakly damaged (Zyryanova et al. 2002, 2007). Eight years after the fire, *Ceratodon purpureus*, fire specialist species typical of the cryolithic area, occupied about 80% of the burned area and prevented both successful restoration of prefire plant species and invasion of the new species. Only *Vaccinium vitis-idaea*, *Vaccinium uliginosum,* and *Ledum palustre* began their regeneration near the bases of larch stems probably from the survived rhizomes. Plant community has not developed fully at this site, since experimental and geometric series distributions differed considerably (plot 3 Tembenchi; Fig. 5.4). Thus, small hillocky microtopography is responsible for rather uniform burning of ground vegetation and slackening of its subsequent restoration.

5.3.2 *Sites Without Microtopography*

We investigated successional sequence of the forest association designated as *Larix gmelinii – Duschekia fruticosa – Ledum palustre + Vaccinium vitis-idaea –* green mosses after a strong running ground fire at three sites where microtopography was not well developed (plots 4–6; Table 5.1). Being typical for the cryolithic area, the old *Larix* forest occupied the upland sites and was considered to be the vegetation composed of a late successional fire species in the region (Abaimov et al. 1997b, 2002). Vegetation of plot 4 was described annually since the time of the fire in 1990, whereas plots 5 and 6 were found as separate stages of the chronosequence at different sites (Table 5.1). All chosen sites were completely destroyed by the running forest fire.

Total number of species in a community decreased 1.4-fold 1 year after the fire, as was shown in the flora of the unburned association (Fig. 5.5). The representatives of such families as Salicaceae, Valerianaceae, Caryophillaceae, Saxifragaceae, Pyrolaceae, and Empetraceae disappeared after the fire, while species of Apiaceae, Fumariaceae, and Onagraceae families newly appeared in the burned area (Zyryanova et al. 2004, 2006). Nontypical of prefire, larch community (composed of *Corydalis sibirica*, *Chrysosplenium alternifolium*, *Erigeron silenifolius*, *Androsace septentrionalis,* and other species) appeared at different postfire years. The process of invasion by new plant species prevailed for 9 years after fire, then the number of invading species decreased (Fig. 5.5). Maximum total number of species in the burned site was 1.2 times greater than that in unburned association 9 years after fire. This pattern resulted from the cyclic development of such sod-forming species as *Calamagrostis lapponica* and *Carex media* and coincided with the period when they lost their positions as strong competitors and dominants. The new plant species (*Achillea asiatica*, *Chamaerion angustifolium*, *Urtica dioica*, *Ribes rubrum*, etc.) occupied the newly released ecological niches and became abundant. Since the sixth year after fire, young larch seedlings established a dense layer of regrowth, completing this process by the 11th–12th year (Abaimov et al. 2001). Shrub cover of alder and willow (primarily *Duschekia fruticosa* and a number

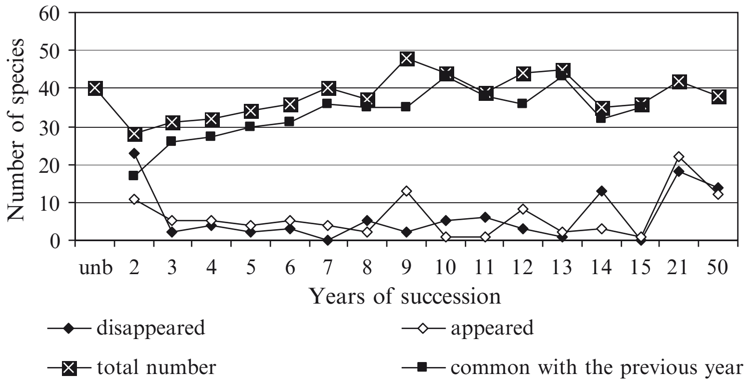

Fig. 5.5 Plant species dynamics at different stages of the postfire progressive succession in the forest site without microtopography. The total number of species, disappeared and appeared plants are shown for each year. The plants which are common to two subsequent years are shown for the early (2–15 years) succession

of *Salix* spp., but *Salix phylicifolia* being the most abundant) may reach dominance of nearly 60%.

In 21 years after a running ground fire, total number of species on the burned area still exceeded that of the prefire community (Fig. 5.5). The species composition was also different: 22 of 42 plants were invaded species (Zyryanova et al. 2004, 2006). But the main layers – the trees, the shrubs, the dwarf-shrubs, and the lichen-mosses – of the vegetative groups were similar to those in the unburned larch forest. The dominants in these layers were the restored plants that were formerly abundant in the stand before the fire (*Larix gmelinii*, *Duschekia fruticosa*, *Vaccinium uliginosum*) accompanied by postfire species of *Betula pendula*, *Salix* sp., *Chamaerion angustifolium*, and *Rubus sachalinensis*.

In 50 years after a fire, the subdominant postfire species disappeared from the species composition of the ground layer. Typical intact dominants kept their positions, but they established more dense layers than in the prefire community. For example, the extent of canopy closure of *Larix gmelinii* and *Duschekia fruticosa* was equal to 40 and 35%, respectively, in the secondary community; whereas 15 and 25% in the intact forest, respectively. The total number of species (38) almost reached the total number before the fire (39) (Fig. 5.5), but the species composition was still different: similarity coefficient (ρ_{sr}) was −0.20 (Zyryanova et al. 2006). Thus, even in a 50-year-old postfire ecosystem, the total number of plant species and their composition differed from those in a prefire larch association, though the forest layers and the dominant species of the community were the same. The spatial structure (vertical and horizontal) of the prefire larch community has been restored within 50 years after a strong running ground fire in the cryolithic area of Siberia. However, species richness and floristic composition of such a community tend to be different from the original forest before the fire. This appears to be a general pattern. Similar results were obtained for tropical forests of central Amazonia (Ferreira and Prance 1999).

Final restoration of the original species diversity and the floristic composition (assumed equal to vegetation of the unburned forest of ca. 90 years old) occurred in the period sometime between 50 and 90 years after the fire (Fig. 5.5). Larch crown and shrub canopies have markedly declined during this time, whereas cover of the ground species has become similar to that of prefire community. As was reported previously (Zyryanova et al. 2002, 2004, 2006, 2007), 90- to 100-year-old larch associations in Siberian cryolithic area represent the ultimate structure of a plant community: the most stable, self-maintaining, and self-reproducing state of vegetational development. Plant species within this community are coadapted to their physical and temporal environment: they may be described as being niche differentiated owing to interspecific competition (Zyryanova et al. 2002).

Postfire dynamics of the species composition was also analyzed with Shannon's diversity index; the index was calculated for the experimental species distribution as well as for the standard geometric series and MacArthur models (Fig. 5.6). Geometric series distribution was established to be a criterion of the community structure development of the larch forest examined. The points where experimental species distribution coincided with the standard geometric series were considered

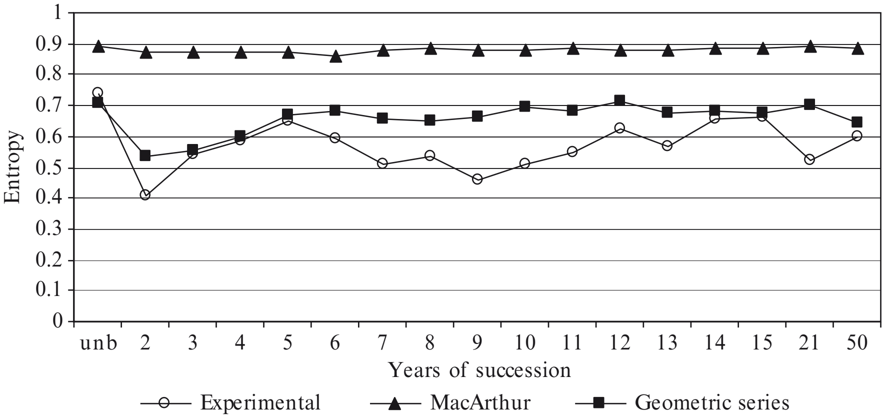

Fig. 5.6 Values of the diversity index expressed as entropy in MacArthur, geometric series, and experimental (=observed) distributions. The diversity indices are scaled with their maximum values for mature larch (unburned) and postfire plant associations at a forest site without microtopography (plots 4–6)

to define secondary plant associations – the key points of the postfire succession. Thus, nine successional stages were distinguished in the long-term process of the forest restoration (Table 5.2). Following a fire, intervening few weeks may be recognized when no live vegetation is present. A similar condition continues to the next year, which is together recognized as stage I (1 year after fire). Here, *Marchantia polymorpha* quickly invades the areas where mineral soil has been exposed by fire. This liverwort and *Corydalis sibirica* develop in stage II (2 years after fire). This annual plant apparently has viable seeds buried in the soil that were stimulated to germinate by fire. Light seeded species such as *Chamaerion angustifolium* (fireweed) is also the usual first invader at this stage. The next three stages in the developing vegetation are dominated by *Calamagrostis lapponica*, which resprouts from the rhizomes. All herbal stages (II–V; 2–5 years) do not form dense soddy mat, and larch seedlings and saplings may be abundant at this time. In about 13 years after fire (stage VI), *Duschekia fruticosa* (alder) with a component of *Salix phylicifolia* (willow) form open shrub cover of as much as 50%. The heavy shrub and seedling canopy greatly reduces the herbaceous strata: its cover drops to less than 7%. Some species of the mature larch forest such as *Vaccinium vitis-idaea* and mosses (*Aulacomnium turgidum* and *Pleurozium schreberi*) become scattered on the mounds. In 14–21 years after fire (stage VII), the main layers of the mature larch association are restored, and *Larix gmelinii*, with a component of birch trees, becomes dominant in the tree canopy. The shrubs form dense layer, while dwarf-shrubs develop a scattered layer. As the stand becomes older, birch trees become less abundant (stage VIII; 22–50 years). Alder is the common shrub; *Ledum palustre* and *Vaccinium vitis-idaea* are the most common dwarf-shrubs at this stage. A dense and thick layer of feathermosses such as *Pleurozium schreberi*,

Table 5.2 Stages of postfire progressive succession in cryolithic area of Central Siberia

Stage	Years after fire	Characteristic vegetation
I	1	Bare surface with separate *Marchantia polymorpha* patches
II	2	Herb-moss species groups with *Calamagrostis lapponica, Corydalis sibirica* and *Marchantia polymorpha* dominants
III	3	*Calamagrostis lapponica - Ceratodon purpureus + Marchantia polymorpha* association
IV	4	*Carex media + Calamagrostis lapponica - Marchantia polymorpha + Ceratodon purpureus* association
V	5	*Carex media + Calamagrostis lapponica − Ceratodon purpureus* association
VI	6–13	Herb-moss association disappeared. *Larix gmelinii, Duschekia fruticosa* and *Vaccinium vitis-idaea* became more widespread and abundant and developed open storeys
VII	14–21	*Betula pendula + Larix gmelinii + Salix phylicifolia + Duschekia fruticosa − Vaccinium vitis-idaea − Pleurozium schreberi + Ceratodon purpureus* association become established. The trees, shrubs, dwarf-shrubs, lichens, and mosses developed closed storeys with prefire and postfire species subdominated. Birch and larch trees overtop the shrubs
VIII	22–50	Prefire dominants (except birch species) become common in the storeys. *Betula pendula + Larix gmelinii - Duschekia fruticosa − Ledum palustre + Vaccinium vitis-idaea - Pleurozium schreberi + Hylocomium splendens + Aulacomnium turgidum* association become established
IX	50–90	Final restoration of prefire plant species composition and cover percentage of the species

Table 5.3 Dominant species of mature larch association and postfire association at the early stages of succession in cryolithic area of Central Siberia

Mature larch association	Postfire associations
Larix gmelinii	
Duschekia fruticosa	*Corydalis sibirica*
Ledum palustre	*Chamaerion angustifolium*
Vaccinium uliginosum, V. vitis-idaea	*Calamagrostis lapponica*
Empetrum nigrum	*Carex media*
Aulacomnium turgidum	*Marchantia polymorpha*
Cladina sylvatica, C. amaurocraea	*Ceratodon purpureus*
C. alpestris, C. rangiferina	*Leptobryum pyriforme*
Cetraria cucullata, C. islandica	

Hylocomium splendens, and *Aulacomnium turgidum* develops by 50 years after fire. Final restoration of the prefire plant species composition and the cover percentage of the species is completed during the period from 50 to 90 years (stage IX). Mature larch forest with a continuous lichen-moss mat develops in about 90–100 years following a ground fire. This is the ninth, and final, stage of the progressive succession (Table 5.3).

5.4 Conclusions

- Ground fires in the cryolithic area of Siberia (i.e., Central Siberia) change floristic diversity of larch associations drastically. In 3–4 years after the fire, the number of vascular plants in a burned area becomes 1.2–1.3 times greater than that of the unburned associations. Both restoration of the prefire species and invasion of the new ones are responsible for such increase in species number. Dominant species of the prefire larch association and subsequent postfire associations are different, particularly during the early successional stages.
- At the early successional stage, mosses are 1.5–3 times less in species number than in the prefire larch association. Feathermosses *Tomenthypnum nitens*, *Dicranum congestum,* and *Aulacomnium palustre* typically begin their restoration, and *Pleurozium schreberi*, *Aulacomnium turgidum,* and *Polytrichum commune* increase their cover drastically, as the canopy of larch seedlings closes in 12–13 years after fire. Species composition in mosses is usually restored by 50 years after a strong ground fire.
- The lichens seem to be much more damaged by fire than the mosses. The number of lichens is two to five times less after fire. Species composition in lichens is restored only in 90 years after fire.
- Generally, the total number of species is 1.1–1.2 times more in sites with and without microrelief than in the unburned association in 9 years after fire. The spot hummock-depression provides faster regeneration of plant species diversity and structure of forest association after ground fires, while small hillocky and elongated stripe-depression microrelief usually delay this process. At the early successional stages, microtopography in northern larch forests sustains plant diversity and increases the number of species and families (Fig. 5.7).

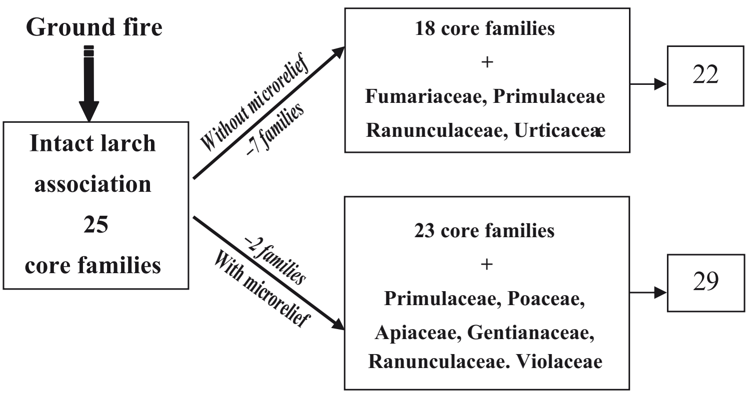

Fig. 5.7 The changes in the composition of vascular plant families at the initial stages of postfire progressive succession. After ground running fires, number of families markedly increased in sites with microtopography than in sites without it (29 vs. 22, respectively)

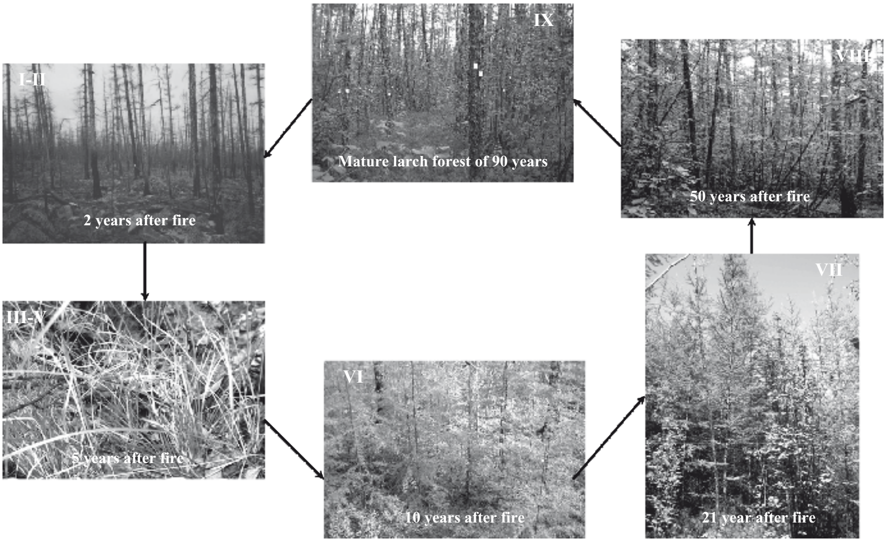

Fig. 5.8 Secondary postfire succession in *Larix gmelinii* (Gmelin larch) forests of Siberian cryolithic zone

- Restoration of plant species' diversity after fire is a long-term process (90–100 years), which may be divided into nine distinctive successional stages.
- Postfire recovery of the larch association described occurs among the even-aged *Larix gmelinii* stands, which represents one of the main trends of postfire succession in the cryolithic areas of Siberia, i.e., progressive succession of forest vegetation without changes in dominant tree species (Fig. 5.8).

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