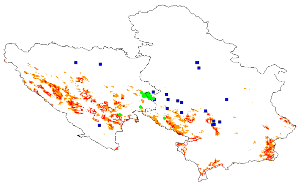

Response of rare and endangered species *Picea omorika* to climate change - The need for speed

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ARTICLE INFO

Citation:
Ivetić V, Aleksić JM (2016) Response of rare and endangered species *Picea omorika* to climate change - The need for speed. Reforesta 2: 81-99.
DOI: http://dx.doi.org/10.21750/REFOR.2.09.24

This article is a part of Proceedings of Symposium "**Forest Adaptation and Restoration under Global Change – the Role of Mountainous Forests**" at "**I International Conference on Research for Sustainable Development in Mountain Regions**" - 5-7 October 2016, Bragança, Portugal, **edited by Antonio Montagnoli and Donato Chiatante**.

Abstract

Serbian spruce (*Picea omorika* (Pančić) Purk.) is a rare and endangered tertiary relict and endemic species, with restricted and fragmented natural range in Serbia and Bosnia and Herzegovina, mainly around the mid-course of the Drina river. Since the middle of the 19th century, its natural range declines constantly, followed by a decline in the number of mature individuals. The decline of this forest species is slow and mainly attributed to poor regeneration and low competing ability. Given the foreseen worsening of the climate in forthcoming decades, this decline can only accelerate. In recent years, dieback related to drought has been observed as response to extreme weather events suggesting that Serbian spruce will face difficulties in adapting to climate change within its natural range. However, successful use of Serbian spruce in Central and Northern Europe indicates potentially large adaptive potential of this species which, along with the high genetic variability, outweigh the limited morphological variation, self-fertilization, and limitations related to the restricted natural range in the first place, and, indicates possible directions of migration in the second place. In this paper, current conservation actions are discussed, and strategies for the species survival in a changing environment are suggested. Since migration and adaptation are the least likely responses of this species to climate change, measures such as assisted migration may be the only strategy which will enable persistence of Serbian spruce. Current conservation programs, limited to in-situ actions, need to be supplemented with ex-situ actions and strategies. In the worst case scenario, i.e. for species such as Serbian spruce which are unable to migrate and/or adapt to changing climate, the most suitable sites should be identified and colonized in order to prevent extinction in the near future.

Keywords

Picea omorika; Climate change; *In-situ* conservation; *Ex-situ* conservation; Assisted migration

Contents

1 Introduction

1.1 Natural range of Serbian spruce

Serbian spruce (*Picea omorika* (Pančić) Purk.) is a rare and endangered tertiary relict and endemic species, with a restricted and fragmented (~ 30 remaining populations) natural range in Western Serbia and Eastern Bosnia and Herzegovina, mainly localized around the mid-course of the Drina river (Figure 1, Table 2). This region represents species long-term, cryptic and last refugium (Aleksić and Geburek 2014). Serbian spruce occupies steep north-to-northwest facing slopes at altitude between 400-1,500 m a.s.l., predominantly on limestone but also on serpentine (one population at site Zmajevački Potok). The non-specific natural site is Crveni Potok, on peat, with 3-5° slope facing NE. Climate within Serbian spruce natural range is typical for mountainous regions, with high snow cover, abundant fogs, average annual temperature around 5-7°C, and precipitation of ~1,000 mm which represents the lower limit for fir, spruce, and Serbian spruce (Gajić et al. 1994).

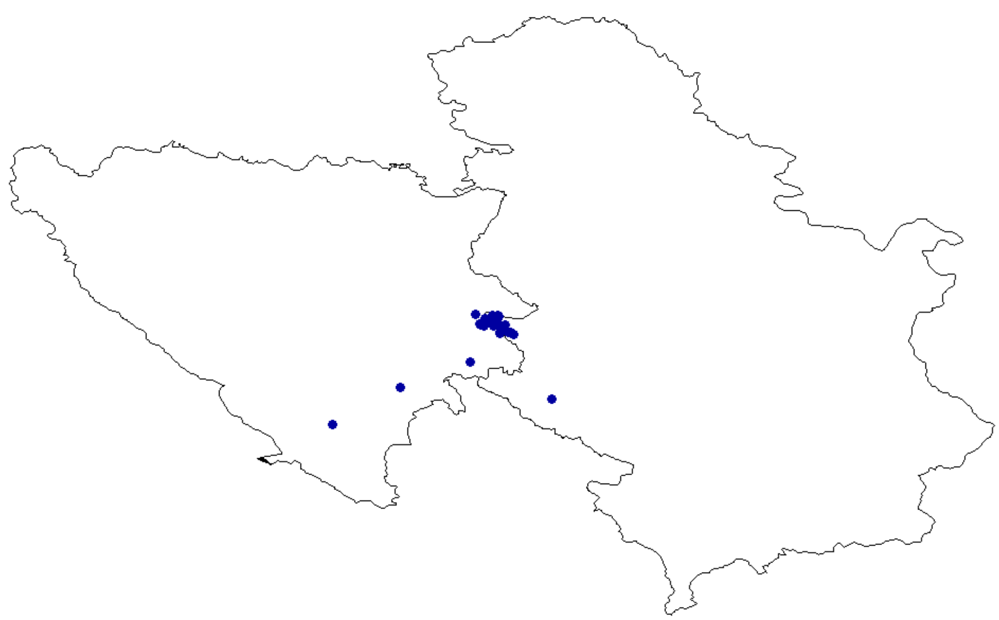

Figure 1. Natural range of Serbian spruce in Serbia (on the right side) and Bosnia and Herzegovina (on the left side), mainly around the mid-course of the Drina river (The Drina river mostly represent the states border).

1.2 Genetics and other features of Serbian spruce

Serbian spruce is predominantly outcrossing species (Kuittinen and Savolainen 1992; Aleksić and Geburek 2014), with reported high self-fertility rates (Langner 1959; Tucović and Isajev 1982; Schemske and Lande 1985; Kuittinen and Savolainen 1992). As a pioneer species, Serbian spruce quickly occupies open areas with abundant number of germinants, which most likely may be produced via both selfing or outcrossing. Kuittinen and Savolainen (1992) reported that Serbian spruce employs other means than early acting inbreeding depression to avoid selfing (e.g. protogyny, spatial isolation of male from female strobili), and, decreased fitness has been observed in inbreds during later ontogenetic stages (Geburek 1986). Thus, it is very likely that selfed trees are eliminated by natural selection early on in the establishment phase. This would explain why in 499 adult individuals, as analyzed by Aleksić and Geburek (2014), none were produced via selfing despite exceptionally low gene flow (pollen and seed flow). These authors state that “more than three generations were required for the exchange of one seed between Serbian spruce populations distant 8 km in average” and report an exceptionally low number of migrants per generation (~4%) based on nuclear data.

Available data on levels of genetic diversity and genetic structure of Serbian spruce natural populations, even for the same type of molecular markers, are seemingly inconclusive. Low genetic diversity was observed at allozyme (Ballian et al. 2006) and cpDNA SSRs loci (Nasri et al. 2008). However, rather high levels of genetic diversity have been found at allozyme loci (Kuittinen et al. 1991) and nuclear EST-SSRs (Aleksić and Geburek 2014), while values for mitochondrial (mtDNA) diversity were moderately high (Aleksić and Geburek 2014). Ballian et al. (2006) reported lack of genetic trends using allozymes versus clear geographic structure with two geographical groups based cpDNA SSRs loci (Nasri et al. 2008), and five genetically distinct entities for nuclear and mitochondrial DNA (Aleksić and Geburek 2014). Possible reasons for the observed discordance of data on Serbian spruce genetic diversity and structuring are discussed by Aleksić et al. (2009).

Serbian spruce can hybridize with other species from *Picea* genus, like Sitka spruce - *Picea sitchensis* (Bong.) Carr. (Langner 1959; Vidaković 1963; Roulund 1971), white spruce - *Picea glauca* (Moench) Voss (Roulund 1971; Mikkola 1972; Nienstaedt 1977; David and Keathley 1996), and black spruce - *Picea mariana* (Mill.) Britton, Sterns & Poggenb. (Nienstaedt 1977), and produce interspecific hybrids. Backcrosses of *Picea sitchensis* x *omorika* with Sitka spruces show better frost resistance and hybrid vigour in the juvenile stage at poor sites in Denmark (Nielsen and Roulund 1992). However, results about the performance of Serbian spruce hybrids with other species are inconclusive.

2 Threats

2.1 Old threats

Kolarović (1951) argued that competition, poor natural regeneration, fires, and illegal harvest are regarded as the main threats to Serbian spruce during the mid-20th century. Since then, Serbian spruce has been protected by the law and thus, illegal harvest has been prevented. The other mentioned threats, however, are still present.

Serbian spruce forms normally pure and rather dense stands, but it may be associated with *Picea abies* (L.) Karst., *Abies alba* Mill., *Fagus sylvatica* L., and *Pinus sylvestris* L., *Pinus nigra* Arnold, *Acer platanoides* L., *Carpinus betulus* L., and *Ostrya carpinifolia* Scop., *Sorbus aucuparia* L. (Jovanović 2000). On slopes facing north occupied by Serbian spruce, the most limiting environmental factor seems to be light, and therefore, the capacity of Serbian spruce to become rapidly photoautotrophic can be decisive to achieve a successful competition for radiant energy (Tucić et al. 2005).

Natural regeneration of Serbian spruce is limited to relatively open sites (Čolić 1957). Following seed dispersal, germination rate is low and the most of germinants in dense forests die during the first year (Ostojić and Dinić 2009), due to the species low additive genetic variance for shade tolerance (Tucić and Stojković 2001). Natural regeneration is lacking on sites with dense herbaceous cover, while it is the most successful in sites where this species is associated with pines because such sites are characterized by a sufficient amount of light at ground level (Ostojić and Dinić 2012). As a pioneer species, Serbian spruce predominates in open sites, but it is usually suppressed later on by shade tolerant species.

Fire represents perhaps the biggest threat to Serbian spruce. Examples of this calamity are large forest fires which occurred in Bosnia and Herzegovina during the year 1947, with the total devastation of 13 stands in Bosnia and Herzegovina and one in Serbia (Fukarek 1956). Another example comes from the deliberately burnt forest which took place in Strugovi during the 1992-1993 conflict (Mataruga et al. 2011). However, Serbian spruce usually is able to re-establish populations in the same site after the fire (Čolić 1987).

2.2 New threats – Climate change and extreme weather events

Projections of the regional climate model forecast for the area of Serbian spruce natural distribution reveal: 1) a general increase of temperature (between 2.4 and 7°C according to the A2 scenario), and 2) a decrease of precipitation with some local variations (Ivetić and Devetaković 2016). Hydrometeorological hazard has changed in South-East Europe (SEE) including a distinct increase in the frequency of summer heat waves (Sippel and Otto 2014). The region had already witnessed some weather extremes in the last 10 years (2007-2016). The summer of 2007 has been the hottest in South-East Europe, with a temperature of 44.9°C, never recorded before in Serbia (data by The Hydrometeorological Service of Serbia 2015). The summer of 2012 has been the hottest in 19 main meteorological stations in Serbia (of 29) since the start of regular measurements in 1848 (Hydrometeorological Service of Serbia, 2013). In 2011, only 63% of the 30-years (1971-2000) average precipitation has been recorded in Serbia (Table 1) (Ivetić 2015). In the spring of 2014, heavy rains caused floods and landslides in Serbia and Bosnia and Herzegovina.

3 Response of Serbian spruce to climate change

In addition to the significant increase of temperature and decrease of precipitation, the biggest challenge for successful regeneration of Serbian spruce will be the frequency, duration, and severity of extreme weather conditions. During 2012, dieback of forests was noticed in Serbia, at a small scale though. This process has escalated in 2013, following the dry three-year period (Ivetić 2015), with dieback of individual trees or groups of trees in Serbian forests for a total of 13,885 ha (PE Srbijašume database). The reported dieback dynamics has followed a similar pattern for all species examined: drought, physiological weakening, disease, pests, and dieback.

In the field, dieback of Serbian spruce has been observed in stands where other species are also dying (spruce, pine, etc.). However, the vulnerability of Serbian spruce is higher than any other species due to its smaller population sizes and lack of a natural regeneration.

Table 1. Annual average temperature and precipitation during a five-year period (2011-2015) in Godovik, Serbia.

Year	Annual average temperature (°C)	Deviation from the normal value (°C)	Annual sum of precipitations (mm)	Percent of average precipitation
2011	9.7	0	460.6	63
2012	10.4	0.7	612.7	84
2013	10.7	1	638.2	88
2014	10.9	1.2	1,121.5	154
2015	10.9	1.2	558.9	81

Figure 2. Dead trees of Serbian spruce in seed orchard in Godovik.

Dieback of Serbian spruce has been reported also in seed orchard in Godovik, Serbia (Figure 2) (more details on seed orchard will be provided in section *4.3 Seed sources – Orchard and stand*). In the last few years, an increase of the number of trees infected by *Armillaria ostoyae* (Romang.) Herink. has been observed with a time-course from infection to lethal outcome spanning around 1-3 years. Serbian spruce is one of the most susceptible species to *Armillaria* infections (Keča 2010), and after a survey carried out during 2014, 14% of the total number of individuals were dead, with an additional 3% of dead trees recorded during surveys conducted in 2015 and 2016 (Jezdimirović 2016). Although the spreading of *Armillaria* in this seed orchard could be limited, the increase in number of dead trees in Godovik indicates clearly what the destiny could be for other populations (both natural and planted). The climate in the area where the seed orchard has been established is warmer (an annual average of 9.7°C the compared to 5-7°C in natural range) and dryer (annual average precipitation of 725 mm during the period 1981-2010 compared to ~1.000 mm in natural range), similar to projection of climate change for region of Serbian spruce natural distribution. In addition, during a five-year period (2011-2015), temperature at the Godovik area has been constantly above, and precipitation below, the normal values (Table 1), with the exclusion of the exceptional year 2014, as described above. Under such unfavorable conditions, Serbian spruce becomes physiologically weak and therefore more susceptible to diseases and pests including *Armillaria ostoyae* (Figure 2).

4 Actions

4.1 *In situ* strategies – Protection and conservation

Since 1950, Serbian spruce in Serbia has been recognized as an endangered conifer and for this reason, all known stands and individual trees are protected (Čolić 1951). Serbian spruce has been listed on IUCN red-list in 1998 first as vulnerable, and then from 2010 as an endangered plant species (Mataruga et al. 2011). In Serbia and in Bosnia and Herzegovina combined there is a total of 3,090 ha of forest reserves with strict protection of Serbian spruce (Table 2). After 40-60 years of protection in Serbia, Serbian spruce stands are mainly in the terminal phase of virgin forests, with an average age of dominant trees of around 200 years (Ostojić and Dinić 2012). However, given the poor natural regeneration of Serbian spruce, the “do not touch” approach is questioned today, and several different measures have been suggested for its conservation.

In some cases, selective removal of individual trees representing Serbian spruces main competitors is recommended in dense forests with the aim to facilitate natural regeneration of Serbian spruce (Ostojić and Dinić 2012; Aleksić and Geburek 2014). However, Fukarek (1956) states that by felling other trees in immediate proximity of Serbian spruce trees could sometimes be fatal because this may cause variations in micro-ecological condition of the site. Nonetheless, the removal of individual trees of competing tree species could be beneficial because it can create gaps with favorable light conditions which are, therefore, suitable for the establishment of Serbian spruce seedlings.

Another possibility for “in situ” conservation is assisted natural regeneration (by planting seedlings) at sites within or in vicinity of the Serbian spruce current natural range which are not occupied by this species currently, but at which Serbian spruce was present in the past. Populations of Serbian spruce at such sites may have been destroyed by fire and/or other calamities, and subsequently occupied by other species. The establishment of even-aged populations during such reintroduction of Serbian spruce into large areas should be avoided. The use of seedlings originating from different population as well as planting of seedlings at different times will improve sustainability of the new forest. Regular planting patterns should also be avoided, and this would result in new forests having a more natural look, as well as provide more favorable conditions to individual seedlings. In hardly accessible sites, direct seeding can be an alternative to planting. In recent years, direct seeding has been recommended as a suitable strategy for the reintroduction of endangered species (Laborde and Corrales-Ferrayola 2012; Atondo-Bueno et al. 2016) either by sowing in open sites or by enrichment planting in secondary forests. In addition, the resilience of artificially established populations within natural range can be promoted by an appropriate provenancing strategy, which will be discussed in section *4.2.2 Assisted migration*.

Table 2. Reserves with natural populations of Serbian spruce.*

	Locality	Area (ha)	Altitude (m a.s.l.)	Slope (°, facing)	Nr. of trees**
	Serbia				
1	Bilo	15.00	1,050-1,300	50-55, NW	4,192
2	Ljuti Breg	12.17	1,100-1,300	35-55, NE	1,319
3	Crvene Stene	43.45	1,000-1,200	N, NE	3,000
4	Studenac	2.74	1,255-1,350	35-60, NW	763
5	Pod Gorušicom	12.00	1,258	65, N	
6	Zvezda	2,584.28	220-1,440	W-NW	50,000
7	Vranjak	3.98	850	35-45, N, NW	442
8	Karaula Štula	9	950	SW	374
9	Ravnište – Kanjon Mileševke	143.71	800-900	45, N	300
10	Crveni Potok	15.43	1,085	3-5, NE	3
11	Zmajevački Potok	3.91	830-850	30-35, N-NE	797
Total area in Serbia		2,846.2			
	Bosnia and Herzegovina				
1	Tovarnica	2	980	N	
2	Karaula Štula	2	950	N	100
3	Božurevac	10	900-1,000	N, NE	
4	Veliki Stolac	10	1,100-1,500	N, NE	3,000
5	Gostilja	50	1,100-1,300	N	1,000
6	Panjak	30	1,250-1,350	N	20
7	Novo Brdo	20	900-1,100	NE	200
8	Pliština	20	1,250-1,450	NE	
9	Strugovi	30	800-1,100	N	100
10	Viogor	40	1,320	N	150
11	Radomišlje - Sokolina	30	1,350	N, NE, NW	
Total area in Bosnia and Herzegovina		244			
TOTAL AREA		3,090.2			

*adapted from Fukarek 1956, Pintarić 1999; Ostojić and Dinić 2012
**there is no consensus on number of individuals

For example, the most threatened Serbian spruce population presently is Crveni Potok, found at peat. There is no natural regeneration at this site, germination rate is low and mortality in the first year after germination is high. Ostojić and Dinić (2009) found six remaining trees at this site, and recommended planting 5-10-year-old seedlings grown from seedlings from nearby stands found on limestone. However, at the same site Aleksić and Geburek (2010) found only three remaining trees, and argued that planting Serbian spruce seedlings at this site would be unsuccessful because this population is actually a good example to demonstrate the extraordinary adaptability of Serbian spruce which survives for a long time and at unfavorable sites such as peat.

Any opportunity to increase the size and the number of populations within Serbian spruce natural range via reintroduction should be exploited. Planting of carefully selected seedlings in sites neighboring current small and declining natural populations could have a positive effect, because, at least theoretically, gene flow from surrounding plantations could increase their effective population sizes.

4.2 *Ex situ* strategies – Transfer and assisted migration

4.2.1 “Traditional” transfer

The success of a planted forest established with transferred planting material is directly dependent on the ability of a forest (population) to adapt to a new environment (Ivetić et al. 2016). Intentional movement of genotypes/genes has to fulfill a number of preconditions and is defined by a number of factors (see Dumroese et al. 2015). Up to date, movement of Serbian spruce reproductive material for planting can be characterized as transfer, e.g. “human-mediated movement of tree germplasm, regardless to geographical scales” (Koskela et al. 2014).

Planting Serbian spruce outside its natural range has a long tradition. In addition to the initial use as an ornamental plant species in parks, Serbian spruce has a long tradition of use in forestry outside from its natural range. Planting outside its natural range started at the end of the nineteenth and the beginning of the twentieth century in: Switzerland (1881 - Meyer 1960), Britain (1889 - Mitchel 1975), Estonia (1890 - Kasesalu 2002), Denmark (1891 in parks, before 1940 in forestry - Møller 2013), Finland (1932, second generation plantation - Kuittinen and Savolainen 1992), and Czech Republic (1934 - Kral 2002). Serbian spruce has been planted in Germany as a popular ornamental tree, much more frequently than other rare species that have been included in the IUCN Red List (Schmidt and Tegeler 2014). It is also one of the tree species most commonly introduced in The Netherlands (Buiteveld 2012).

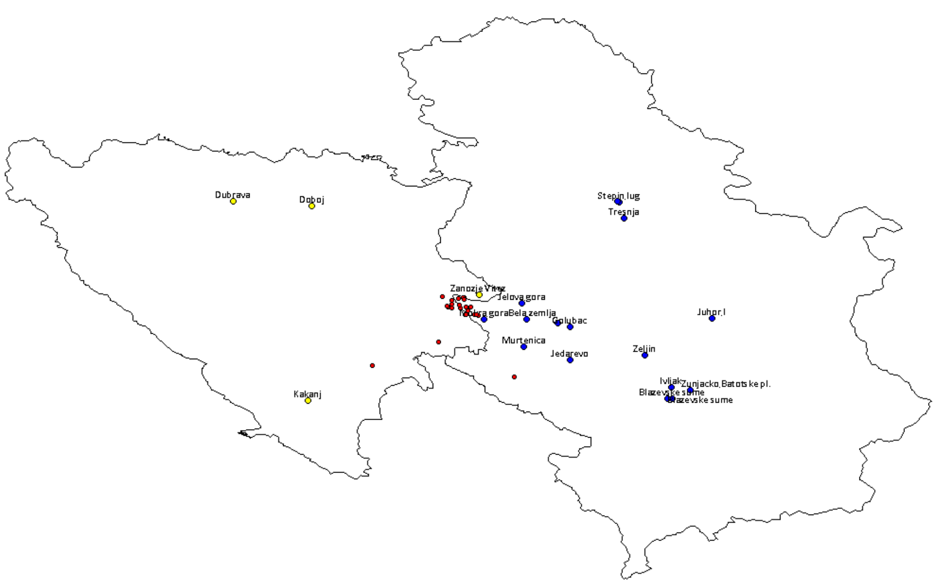

Figure 3. Natural (red dots) and planted (blue dots) populations of Serbian spruce in Serbia and Bosnia and Herzegovina (yellow dots).

Today, in Serbia and Bosnia and Herzegovina, plantations of Serbian spruce for forestry amount to only 35 ha (Figure 3, Table 3). Only a few plantations are more than 40 years old, and most of them are situated in sites with an unsuitable altitude and slope.

Table 3. Planted populations of Serbian spruce in Serbia and Bosnia and Herzegovina.

	Locality	Surface	Altitude (m asl)	Slope (°, XXX)	Age	D	H
			Serbia				
1	Juhor I	1.21	590-610	5, W	14		
2	Žunjačko Batotinske Planine	0.25	810	10-15, W	12		
3	Blaževske Šume	1.77	930-980	15-20, NE	4		
4	Blaževske Šume	3.9	1,050-1,140	20-25, E	16		
5	Ivljak	0.78	880-915	15-20, NW, NE	13		
6	Željin	0.6	1,090-1,130	5-10, N	33		
7	Golubac - Dubavac	0.66	610-620	5-10, N	31		
8	Murtenica	2.56	1,260-1,290	5-10, NE	40	16	14,9
9	Venac - Blagaja	2.7	420-460	5-10, NW	27	12	8
10	Jelova Gora	1	950-1,000	5	28		
11	Mokra Gora - Kršanje	0.74	1,050-1,080	15-20, SW, SE	40	13	11
12	Bela Zemlja	0.53	715-720	5, NW	50	17	13
13	Trešnja	0.6	250	5-10, SE	35	17	12
14	Stepin Lug	0.08	130-160	10-15, E	30	16	16
15	Stepin Lug	0.02	230-240	0-5, S	29		
16	Čemerno	1.03					
Total in Serbia		18.43					
			Bosnia and Herzegovina				
1	Kakanj	8.5	710				
2	Dubrava	0.33	300	S	40	22	15
3	Zanožje Vitez	0.6	860	NE	25	15	10
4	Doboj	7.5	220				
Total in Bosnia and Herzegovina		16.93					
TOTAL AREA		35.36					

In most of these transfers, the origin of planting material is not traceable (in the case of recent plantations in Serbia, the seeds used for their establishment had been collected in the Godovik orchard) and the relative size of established populations is small, ranging from a few dozen to a several hundred individuals. Nevertheless, these populations can play a significant role in Serbian spruce preservation. In natural populations, no positive correlation between *He* and population sizes has been found (Aleksić and Geburek 2014). When properly established, a similar situation can be expected in artificially established populations, considering that there is no conclusive evidence that genetic diversity is reduced in planted forests (as reviewed by Ivetić et al. 2016). A good example of an artificially established population of Serbian spruce used as seed source, has been reported by Kuittinen et al. (1991). The plantation in Punkaharju, Central Finland (initially comprising 100 trees), has been established with seeds collected in the Elimäki plantation, which in turn has been established with seeds collected in natural population in Bosnia and Herzegovina. Expected heterozygosity, assessed using allozymes, in population cultivated for two generations in Finland (*He*=0.15) was similar to that found in natural population (*He*=0.13) in Bosnia and Herzegovina (Kuittinen et al. 1991, Table 5). Despite this good example, any use of plantations as seed source for production of forest reproductive material needs to be tested for both: a) the level of genetic diversity and b) the effective population size.

Although reports Serbian spruce tolerance to cold affecting the whole root systems (Bigras et al. 2001), to frosts (Meyer 1960; Nymoen 1978; Vidaković 1991), to air pollution (Dallimore et al. 1967; Kasesalu 2002), and to extremely harsh environmental conditions (Kuittinen et al. 1991) are available, the knowledge on adaptive genetic variation of this species is still lacking.

Table 4. Planted populations of Serbian spruce far away from its natural range.

Locality, Country	**Use**	**Performance**	**Compared to**	**Site**	**Source**
Saxony, Germany	Plantation.	Inferiority in height, no difference in diameter, greater resistance to snow, ice, and frost.	*Picea abies*	Different.	Meyer 1960
Sokolov, North Bohemia, Czech Republic	Reclamation after brown coal mining.			Spoil heap.	Cejpek et al. 2013
Britain	Plantation.	Poor.		Exposed.	Nixon and Tyler 1993
Estonia	Plantation.	Fast-growing and cold-resistant.			Sander and Meikar 2009
Southern Finland	Plantation.	Good	Seven species.		Silander et al. 2000 cited in Sander and Meikar 2009
Britain	Plantation.	Good survival and height growth.	Several species.	Peat.	Zehetmayr 1954
Faroe Isles and at the Greenland		Extremely slow growth.			Ødum 1991
Jaervselja, Estonia	Plantation.	Immune to fungus diseases and insect damages, frost-hardy, tolerant to smoke.		Different.	Kasesalu 2002
Křtiny, Czech Republic	Plantations	Good	*Picea abies*	Different.	Král 2002
Coastal areas of Norway	Plantation.	Frost hardy and resistant to sea winds, superior height increment.	*Picea abies*	Drained bog and heathland.	Nymoen 1978
USA		Well at three sites in Minnesota and at the Wisconsin site, but grew poorly elsewhere.			Widrlechner et al. 1992

The success of Serbian spruce plantations outside of the species natural range is still uncertain (Table 4), due to: 1) different environment conditions, 2) type of establishment goals, 3) management measures, and 4) reproductive material provenience. Recent data indicate that a fundamental niche of Serbian spruce may be much larger than a man-realized niche (as determined by Gray and Hamann 2011). These populations could be considered as “unintentional experiments in progress” and thus, they represent a solid lab bench for future studies to address questions related to the still unknown adaptive potential of Serbian spruce (even if these trials lack a general plan and a set of rules). Aiming to test adaptive genetic variations of Serbian spruce, comprehensive trials should be established at an international level.

4.2.2 Assisted migration

In analogy with other pioneer plant species, it has been reported that a physiological optimum of Serbian spruce may also be outside of its natural range (Jovanović 2000). However, the risk of maladaptation in transfer of forest reproductive material increases with length of distance that can be: geographic, climatic, and/or temporal (Williams and Dumroese 2013). All three distances should be considered for any future transfer of Serbian spruce. Given the availability of suitable planting sites, successful persistence in changing environment requires knowledge on genetic variation and local adaptation of targeted species, especially for those characterized by small populations and limited or disjunctive ranges (Ivetić and Devetaković 2016).

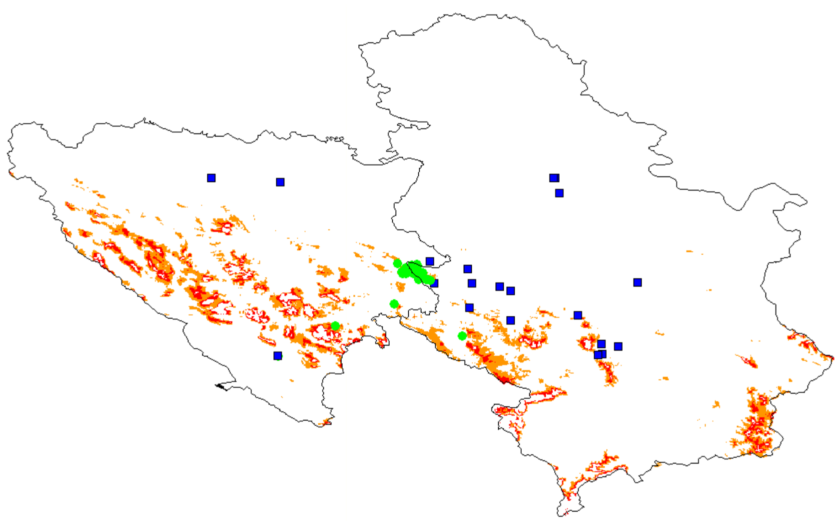

Figure 4. Areas with suitable sites for future plantations of Serbian spruce (orange - elevations of 1,200-1,400 m a.s.l., red - 1,400-1,600 m a.s.l.), natural populations (green circles), and plantations (blue squares). It is evident that sites with supporting environment for Serbian spruce in the future are outside its current natural range, and that current transfer programs had missed the target.

Considering the disproportionate difference in pace between climate change and migration rates of tree species, assisted migration is a suitable strategy which may provide survival of species in terms of rapid climate change. However, this strategy should be implemented at a small scale (Ivetić and Devetaković 2016). For example, according to projections of the regional climate model, suitable sites for Serbian spruce in the future will be on altitudes between 1,200-1,600 m a.s.l. (Figure 4). Within this altitudinal range, suitable sites should be also selected by taking into consideration: 1) the level of precipitations, and 2) other ecological parameters (such as soil type - limestone, north facing slopes, and plant species associations). After selecting suitable sites, the best matching provenances should be used as a source of forest reproductive material. Serbian spruce shows a strong uniformity of morphological characteristics (Vidaković 1982), but with individual phenology differences, like bud flushing (Langer 1959). In addition, selection of the best matching provenance to a specific site is possible due to high differentiation of populations being at a distance of a few kilometers or less, which were characterized as independent gene pools at the nuclear DNA level (Aleksić and Geburek 2014).

Two approaches for matching provenances to planting sites facing climate change are suggested: 1) the use of climate envelope modeling which compare the climate of sites of seed-source populations and potential planting sites (Beaulieu and Rainville 2005; Gray and Hamann 2011; Potter and Hargrove 2012; Isaac-Renton et al. 2014; Gray and Hamann 2013), and 2) the use of empirical-response functions, which are based on correlations between quantitative traits and climate variables using climate-response functions (Wang et al. 2010; Hamann et al. 2011; Chakraborty et al. 2015). Empirical approaches relying on characteristics of seed source populations appear to be more successful than those based on climate envelope approach (Chakraborty et al. 2015). However, both of these approaches should be tested for Serbian spruce. In a changing environment, provenance should be matched to site both spatially and temporally (Ivetić and Devetaković 2016). Selection of sites for Serbian spruce should be based also on estimates whether environmental conditions in the forthcoming period would be able to enable persistence of populations in the future, and thus, sites having environmental conditions which may fail to provide seedlings survival in the future should be avoided. Jovanović (2000) argued that the current limited natural range of Serbian spruce is mainly the result of the species poor competing ability, but it may also depend on the potential of seedlings to survive.

In addition to matching provenance for focal site, many other provenance-strategies have been suggested in possible response to predicted climate change (Ivetić and Devetaković 2016). No single strategy is likely to work universally, so selection of provenance should consider genetic variation of plant species and local adaptation combined with climate projections for focal site. For Serbian spruce, the composite (Broadhurst et al. 2008; Breed et al. 2012), admixture (Breed et al. 2012), and climate-adjusted provenancing (Prober et al. 2015) should be considered. These three provenancing strategies may, on one hand, increase the risk of maladaptation and outbreeding depression, and, on the other hand, enhance evolutionary- and climate-resilience, by mixing genotypes pre-adapted to potential micro-climate conditions and by introducing more additive genetic variation.

4.3 Seed sources – Orchard and stands

The current level of Serbian spruce protection does not allow collection of seed in natural populations except for research purposes. At the same time, natural populations decline due to poor natural regeneration and drought-triggered dieback. In such a paradox situation, seed orchards offer a continuous supply of seeds of controlled origin, and planted populations used as seed stands offer a cheap source of seeds. There is only one registered seed orchard and three seed stands of Serbian spruce at this moment, located in Serbia.

The existing seed orchard of Serbian spruce in Godovik, Serbia (43°46’54” N, 20°02’57” E, 440 m a.s.l.) was established in 1987, from 5,956 genotypes from 50 halfsib lines (Tucović and Isajev 1988). Drought-triggered process of dieback in this orchard is discussed in section *3 Response of Serbian spruce to climate change*.

The initial assumption that high levels of genetic variability and adaptive potential of Serbian spruce have been captured and maintained within this seed orchard is questionable. This is because this seed orchard has been established with seeds from three planted cultures (Bela Zemlja, Popova Luka, and Šargan), but all three cultures were established with seeds from a single Serbian spruce population at locality Zaovine (Isajev 1987). Nonetheless, expected heterozygosity in seed orchard assessed using allozymes (Milovanović and Šijačić-Nikolić 2010) is similar to those found in natural and planted populations of Serbian spruce, which is consistent with eight studies which compared heterozygosity in seed orchards and natural populations of different tree species (as reviewed by Ivetić et al. 2016).

Table 5. Levels of Serbian spruce expected heterozigosity at the nuclear DNA level, in natural populations, plantation and seed orchard.

He	Marker	Population	Source
0.13	19 enzyme loci	Natural	Kuittinen et al. 1991
0.15		Cultivated	
0.067	16 isozyme loci	Natural	Ballian et al. 2006
0.776	five nuclear microsatellites (EST-SSRs) and a mitochondrial (mtDNA) locus	Natural	Aleksić et al. 2009
0.146	16 isoenzyme loci	Seed orchard	Milovanović and Šijačić-Nikolić 2010

Figure 5. Seed orchard of Serbian spruce in Godovik, Serbia.

This seed orchard needs intensive disease control, and its use should be limited to research purposes only. Establishing a program for controlled pollination can provide a certain amount of seeds for a future planting program with a reduced risk of inbreeding depression. Seeds from open pollination should be avoided in the production of seedlings to be planted in forests because of the possible risk of obtaining a high portion of inbreeds. In fact, due to favorable conditions during nursery production, inbreed individuals could survive and be planted. Although these inbreeds can be eliminated by selection during the first three years of the establishment phase (Muona et al. 1987), we believe that this practice is an unnecessary waste of resources.

The seed stand of Serbian spruce in Bela Zemlja, Serbia (43° 48′ 55″ N, 19° 48′ 10″ E, 710 m a.s.l.) represents one of the early attempts of the production of Serbian spruce reproductive material outside of its natural range. The top of some trees were pruned with the aim of producing a larger number of strobili and to facilitate cone collection. This attempt to promote productivity has not been followed by a suitable silviculture practice which would enable obtaining a reduced number of overgrown trees, and a limited effective population size. Nonetheless, this stand is healthy, and during the 2016 survey, no dieback was found (Figure 6).

Figure 6. Seed stand of Serbian spruce in Bela Zemlja, Serbia.

The seed stand of Serbian spruce in Dubrava, Republic of Srpska, Bosnia and Herzegovina, (44° 44′ 54″ N, 17° 30′ 59″ E, 300 m a.s.l.) is ~40 years old. Seed stand has been planted with seeds from Višegrad and covers 0.33 ha (Matarga et al. 2005).

The seed stand of Serbian spruce in Zanožje Vitez, Republic of Srpska, Bosnia and Herzegovina, (44° 0′ 42″ N, 19° 26′ 14″ E, 860 m a.s.l.) is ~30 years old. This Seed stand has been planted with seeds from an unknown origin, it covers 0.6 ha (Matarga et al. 2005), and trees are in good condition.

The state of the art of production of Serbian spruce reproductive material emphasizes the need for rapid actions. Collection of seeds from natural populations should not only be allowed, but also encouraged, and, when necessary, to become compulsory. Collected seeds should be used for seedling production and storaged in seed banks. New seed orchards (both generative and clonal) need to be established and designed to maintain a level of genetic diversity present in natural populations, with a special target for rare alleles. In cases of populations with only a few remaining individuals, the last resort for reproduction may be in vitro tissue culture (micropropagation and/or somatic embryogenesis, Mihaljević and Jelaska 2005, Hazubska-Przybył and Bojarczuk 2008).

5 Conclusions

Competition, poor natural regeneration and fires remain the major threats for Serbian spruce populations. Dieback induced by climate change is a new threat whose severity for Serbian spruce is much higher than for some other tree species because of the small size of its populations and lack of natural regeneration. Assisted natural regeneration by planting seedlings within and/or nearby species current natural range and assisted migration to sites able to provide Serbian spruce persistence in the future, are both suitable strategies in terms of climate change. These actions are necessary especially if one considers the effect of factors such as: 1) the increasing pace of climate change, and 2) the low migration rate of this tree species. Planting Serbian spruce outside of its natural range has a long tradition. These populations can be seen as “unintentional experiments in progress” and they could represent a solid foundation for future research on Serbian spruce adaptive potential. Collection of seeds from natural populations needs to be encouraged and it should even become compulsory. Collected seeds should be used for seedling production and storaged in seed banks. New seed orchards need to be established and designed to maintain a high level of genetic diversity which characterizes natural populations, with a special aim of the conserving of rare alleles.

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