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Survival and vitality of a macrolichen 14 years after transplantation on aspen trees retained at clearcutting

Lena Gustafsson [a,*], Katja Fedrowitz [a], Per Hazell [b]

[a] Swedish University of Agricultural Sciences, Department of Ecology, P.O. Box 7044, SE-750 07 Uppsala, Sweden
[b] Swedish Forest Agency, P.O. Box 1350, SE-751 43 Uppsala, Sweden

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ABSTRACT

Industrial forestry has caused large biodiversity changes in European boreal forests. One recently introduced conservation measure in production forestry is retention of trees at clearcutting to benefit flora and fauna. Aspen *Populus tremula* is often retained for conservation purposes since it is a key tree species for biodiversity with many associated species, a number of which are red-listed. Still, the importance to biodiversity of aspen trees retained at harvest is largely unknown. In 1994, a transplantation experiment with the old-growth forest indicator lichen *Lobaria pulmonaria* was set up on 280 aspens at 35 sites in east-central Sweden with a total of 1120 transplants, with the aim to assess the habitat suitability of retained aspens following harvest. After 14 years 23% of *L. pulmonaria* transplants remained, with a significantly higher survival on retained aspens than on aspens in the surrounding forest, especially on the northern side of stems. Transplants were also more vital on northern than on southern sides of stems. There was no difference in survival or vitality of transplants between dispersed aspens and aspens in groups. Results largely agreed with a re-inventory made already after two years but the importance of the north side of retention trees became evident for species survival only after 14 years, indicating that to gain deeper insights longer time-spans may be necessary. This study, which is the longest lichen transplantation time-series from a well replicated experiment so far published, shows that retention of trees at harvest may be an efficient conservation action.

1. Introduction

The global trend of declining biodiversity (Butchart et al., 2010) is evident also in the boreal forest biome, which amounts to about 30% of the world's forest area, running circumpolar on the northern hemisphere (Hansen et al., 2010). Clearcutting, i.e. removal of all trees at harvest, is a main forest operation technique for industrial forestry in boreal forests. To counteract associated negative ecological effects, retention approaches have been introduced during the last two decades implying that e.g. some living old trees are left at harvest (Gustafsson et al., 2012). A key function of retained trees is lifeboating, i.e. to provide refugia for species that would otherwise be lost at harvest (Franklin et al., 1997). Studies on the retention approach in forestry point to positive biodiversity effects compared to traditional clearcutting (Rosenvald and Lõhmus, 2008), although low retention levels in Fennoscandia raise questions regarding its effectiveness to promote flora and fauna (Gustafsson et al., 2010).

European aspen *Populus tremula* L. and the closely related and ecologically similar Quaking aspen *P. tremuloides* Michx. in N. America are distributed over wide areas on the northern hemisphere (Farmer, 1997; Worrell, 1995), and are key hosts for hundreds of species (Kouki et al., 2004; Rogers and Ryel, 2008; Lõhmus, 2011), including red-listed species (Tikkanen et al., 2006). In Sweden it is a minority tree species comprising on average only 1.5% of the total tree volume on the productive forest land (Swedish Forest Agency, 2012). Aspen is prioritized as a retention tree and often large-diameter aspens are left un-harvested at clearcutting. There are uncertainties to which extent species associated with old, more closed forests can survive on retained aspens in the relatively large open environment after final harvest.

Transplantation of lichens is a common tool in research to monitor air pollution (e.g. Nimis et al., 2002), to study growth and ecology of species (e.g. Coxson and Stevenson, 2007a,b), and to assess if the technique can be used to relocate threatened species (e.g. Lidén et al., 2004). Most studies so far embrace only short time periods, e.g. up to one year: Sillett and McCune (1998), Gauslaa et al. (2006) or two to three years: Scheidegger et al. (1995), Keon and Muir (2002). The longest time-series published to date is a study on *Lobaria amplissima* (Scop.) Forssell on old deciduous trees in N. England, starting with 14 transplants of which six remained after 20 years (Gilbert, 2002). Very few studies on retention trees have used an experimental approach including transplantation. One exception is a study by Hazell and Gustafsson (1999) in which

* Corresponding author. Tel.: +46 (0)18 672747; fax: +46 (0)18 672890.
E-mail address: lena.gustafsson@slu.se (L. Gustafsson).

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the macrolichen (large lichen, as opposed to small microlichens) *Lobaria pulmonaria* L. Hoffm. and the bryophyte *Antitrichia curtipendula* (Hedw.) Brid. were transplanted to aspens in clearcuts, as indicators for habitat suitability of retention trees to sensitive species, with adjacent forest trees as control. Two years after transplantation, distinct patterns emerged with high survival and vitality of both species on clearcut trees. The short time-span restricts conclusions though, and uncertainties have remained whether this is a long-lasting response. Transplants in long time-series are likely to be exposed to large variations in environmental conditions, such as altered microclimate in forest successions following clearcutting, due to change in tree density. They may also be affected by biotic interactions like competition from mosses. We here report a re-inventory of the *L. pulmonaria* transplantation experiment of Hazell and Gustafsson (1999), 14 years after its initiation and with an original sample size of more than 1100 transplants on 280 aspens at 35 sites. It is the longest lichen transplantation time-series so far published from a well replicated experiment. Our main question was if *L. pulmonaria* is able to survive, and if so, how vital it will be on aspen trees retained at final harvest in comparison with forest trees. Other important questions were: What are the differences in survival and vitality of transplants between scattered aspens and aspens retained in small groups?, What is the effect of transplantation occasion (spring or autumn)?, and Do response patterns found after the first inventory two years after transplantation correspond to those 12 years later? Our primal interest in the transplantation outcome was based on an aspiration to gain knowledge necessary for the formulation of more specific advice on how to retain aspen trees at final harvest to benefit biodiversity.

2. Materials and methods

2.1. The study species L. pulmonaria

L. pulmonaria is a large, epiphytic, foliose, macrolichen with a total distribution area embracing Europe, Asia, Africa and N. America (Yoshimura, 1971). In boreal Fennoscandia it mainly grows on aspen *P. tremula*, goat willow *Salix caprea* L., and *Sorbus* species (Jørgensen and Tønsberg, 2007), and is most abundant in old forest (e.g. Gjerde et al., 2012). The species disperses mainly vegetatively (isidia, soredia), and rarely sexually with spores. *L. pulmonaria* has declined drastically during recent decades in Europe due to forest management and air pollution (Gaio-Oliveira et al., 2004) and possibly also due to old forests becoming denser (Gauslaa et al., 2007). It is today found in small and isolated populations, and is red-listed in several countries, among them Sweden (Gärdenfors, 2010). The species is commonly used in lichen transplant experiments (e.g. Scheidegger, 1995; Gaio-Oliveira et al., 2004; Gauslaa et al., 2006). It has also since almost two decades been used as an indicator species to identify forest habitats with high conservation value in Sweden, as field experience has shown that it reflects the presence of other uncommon and declining species (Nitare, 2005). There are also indications that the species may reflect high conservation values at the landscape scale (Kalwij et al., 2005). At the initiation of our transplantation experiment in 1994, *L. pulmonaria* was not red-listed in Sweden (Databanken för hotade arter and Naturvårdsverket, 1990).

2.2. Study area and experimental design

The study area is located in the hemi-boreal zone (Ahti et al., 1968) in East-Central Sweden (60°02′N, 18°22′E). The proportion of forest >80 years old in the region is 24%, with Norway spruce *Picea abies* (L.) H. Karst. and Scots pine *Pinus sylvestris* L. being the dominant tree species, but the proportion of aspen is unusually high, 4% (Swedish Forest Agency, 2012). Altogether 1120 pieces of *L. pulmonaria*, each about 6 cm^2 large, were transplanted in spring and autumn of 1994 to 280 aspens at 35 sites (Table 1). Each site consisted of a forest and a clearcut, with four receiver aspen in each, i.e. altogether eight trees per site. In 19 clearcuts the receiver trees were solitary (scattered) and in 16 sites they occurred in groups of broad-leaved trees (grouped: >3 aspens >18 cm diameter at breast height and <15 m from each other). The 35 sites were situated within an area of 1900 km^2, with an average distance between them of 24.7 km (range 0.4 - 65 km). In spring as well as in autumn of 1994, two transplantations were made per tree, one on the north and one on the south side of the stems 140 to 180 cm above ground level, amounting to a total number of four transplants per tree. The thallus pieces were attached to the stem with the help of a plastic net (6 × 6 cm with 1 × 1 cm meshes) and metal staples to the bark. Each sample was sprayed with tap water immediately after transplantation.

Table 1
Numbers of receiver trees and *Lobaria pulmonaria* transplants in the different retention types at different years. Transplants include all survived transplants, i.e. exclude those that died or disappeared from tree fall, etc.

	Scattered	Grouped	Forest	Total
Original no of receiver aspens 1994	76	64	140	280
No of aspens with transplants 1996	74	64	132	270
No of aspens with transplants 2008	65	50	93	208
Original no of transplants 1994	304	256	560	1120
Transplants in 1996	252	234	462	948
Transplants in 2008	116	77	61	254

2.3. Assessment of survival and vitality of the transplants

All transplantation sites were visited in summer 1996 and spring 2008 to visually evaluate survival and vitality of the transplants. Prior to evaluation, transplants were sprayed with water in order to enable relevant comparisons since dry and wet *L. pulmonaria* thalli differ in color. If any thallus part remained, the transplant was judged as having survived. If ⩾50% of a survived thallus was in a viable condition (i.e. giving a healthy impression with a green, intact surface without necrosis or signs of damage), the transplant was assessed as being vital. Some transplants were lost due to tree fall, but in 1996 altogether 270 (96%) and in 2008 altogether 208 (74%) trees remained and transplants on these were surveyed (Table 1).

2.4. Control transplantation at collection site

During the setting up of the experiment in 1994, a control transplantation was made at the site of lichen collection, Skånberget, Ramsjö, in the province of Hälsingland, in south boreal Sweden, ca 300 km north of the experimental area. On the north and south sides of 20 trees material of two types was mounted, such that had been frozen for more than one month, i.e. resembling the treatment in the experiment, and also fresh material, in total amounting to 80 transplants. The survival and vitality of these transplants were re-assessed in August 2008.

2.5. Data analysis

Generalized linear mixed models (GLMMs) with logit link functions and Laplace approximation (Bolker et al., 2009) were first applied to test the effect of tree retention, aspect, and transplantation time for transplant survival and vitality in 2008, and second to assess if there was a significant difference in the variables that described survival and vitality in both survey years. The effect of tree retention was tested in two different models, one testing if transplant survival and vitality differed between trees in the forest and clearcut, and the second one testing if there was a difference in transplant survival and vitality between grouped and scattered retention trees.

The following binary response variables (1/0) were used: survival was defined as the transplanted thallus being present (1) or absent (0), and vitality as ⩾50% of the thallus being vital (1) or <50% of the thallus being vital (0).

The global start model for the data of 2008 included forest stand and tree as random factors, and aspect (north or south), forest type (forest or clearcut) or clearcut type (grouped or scattered retention trees), tree diameter (measured in 1996), and transplantation time (spring 1994 or autumn 1994) as fixed effect variables. In the second model, survey year (1996 or 2008) was used as an additional fixed effect variable. Tree diameter was not used in this model since we were not interested if the effect of tree diameter had changed between both survey years. For better comparison between the two survey years we also tested a third model, including only the data of 1996, but running the model in the same way as described for the data of 2008. This was done since the data analysis in Hazell and Gustafsson (1999) used a different statistical approach. Biological meaningful interaction terms were added and all fixed explanatory variables in the interaction terms were centered and scaled (in the case of tree diameter) in order to achieve biologically interpretable estimates (Schielzeth, 2010). Akaike's Information Criterion (AIC, or AICc for small sample sizes) and Akaike weights were used to assess the relative strength of support for all biologically considerable models, given the chosen explanatory variables (Akaike, 1974; Burnham and Anderson, 2002). Since our final models (if there was more than one) did not differ substantially we only report the model estimates for the model with the lowest AIC (AICc, respectively; Bolker et al., 2009).

We used the statistical software R 2.13.0 (R Development Core Team, 2011) and the add-on packages lme4 (Bates et al., 2011) and MuMIn (Bartoń, 2011).

3. Results

3.1. Survival and vitality of transplants over time

From the original number of *L. pulmonaria* transplants in 1994 (1120), 28% (313) were lost due to tree fall or that the transplant net had fallen off, and from the remaining 807 transplants 69% did not survive (no thallus remained) 14 years after transplantation (Table 1). In 1996, 90% of remaining transplants had survived on clearcuts and 88% in forests, compared to 44% and 17% in 2008, respectively. In 1996, 69% of the remaining transplants on clearcuts and 61% in forests were classified as being vital (⩾50% of a survived thallus in a viable condition), compared to 70% and 74%, respectively, in 2008.

3.2. Differences between retained trees and forest trees, including effects of aspect

After 14 years (2008) 61% of all transplants on northern sides on clearcut trees had survived and 26% on southern sides of clearcut trees, while 16% had survived on northern sides and 17% on southern sides of forest trees (Fig. 1). The proportion of transplants assessed as vital was 76% on northern sides of clearcut trees and 57% on southern sides, and 76% on northern sides of forest trees and 72% on southern sides (Fig. 2).

The results of the GLMM showed that survival was significantly higher on clearcuts and there especially on northern sides of aspen trees, compared to southern sides or in the forest (Fig. 1 and Table 2). Vitality of transplants in 2008 was significantly higher on northern sides compared to southern sides in all trees (Fig. 2 and Table 2). Tree diameter improved the models for survival, but the variable was not significant in 2008.

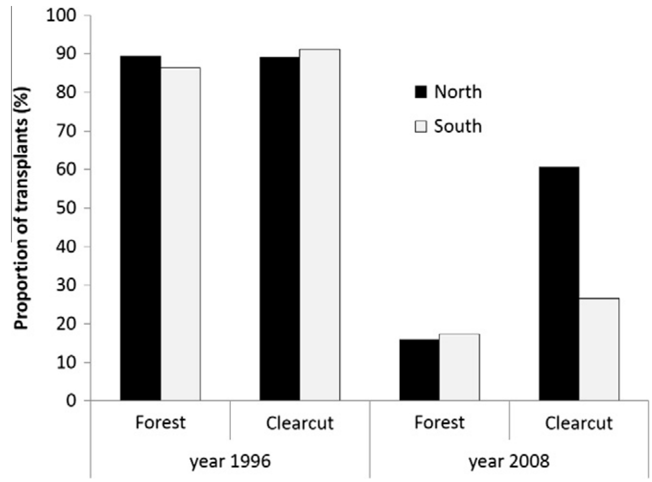

Fig. 1. Proportion of transplants that had survived on north and south sides of trees in clearcuts and forests, respectively, two and 14 years after transplantation.

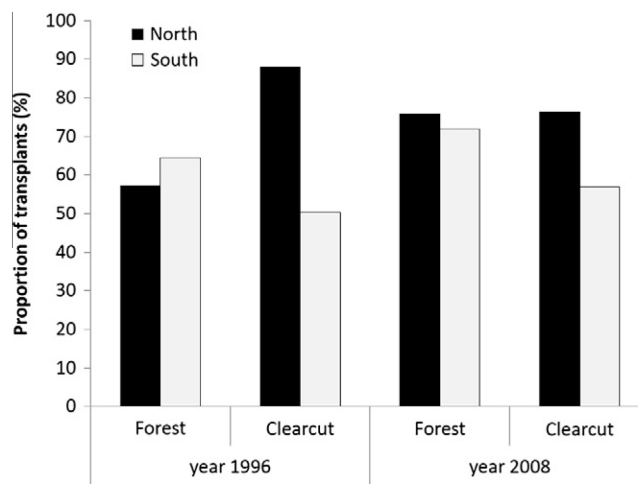

Fig. 2. Proportion of transplants with ⩾50% vitality on north and south sides of trees, respectively, in clearcuts and forests, two and 14 years after transplantation.

3.3. Differences between grouped and scattered retention trees

In 2008, 40% of transplants on trees in groups and 47% on scattered trees on clearcuts had survived after 14 years. Of these 74% and 68%, respectively, were classified as vital. Differences between types of retention trees were not significant, neither for survival nor vitality.

3.4. Effect of transplantation occasion

In 2008, survival of autumn transplants was 36%, which was significantly higher than for spring transplants, 27%. For vitality there was no significant difference between spring and autumn transplants, of which 75% and 68%, respectively, were assessed as vital (Table 3).

Table 2
Model estimates of the parameters explaining survival and vitality in 1996 and 2008. Trans. time = transplantation time.

	Survival 1996		Survival 2008		Vitality 1996		Vitality 2008	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
(Intercept)	3.42***	0.28	−2.00***	0.36	1.14***	0.20	1.17***	0.34
Forest type CLEARCUT	0.54	0.37	3.52***	0.57	0.92***	0.28		
Aspect NORTH			1.52***	0.26	1.49***	0.21	1.14***	0.36
Trans. time AUTUMN	1.37***	0.26	1.00***	0.24	1.57***	0.19		
Tree diameter	−0.42*	0.20	−0.44	0.28				
Forest type:Aspect			3.20***	0.53	3.78***	0.41		
Forest type:Trans. time					2.07***	0.38		

* $p < 0.05$.
*** $p < 0.001$.

Table 3
Model estimates of the parameters explaining survival and vitality for both survey years combined. Significant *p*-values (<0.05) are shown in bold. Trans. time = transplantation time.

	Survival			Vitality		
	Estimate	SE	*p*-value	Estimate	SE	*p*-value
(Intercept)	1.50	0.29	**<0.01**	1.09	0.19	**<0.01**
Survey year 2008	5.56	0.27	**<0.01**	0.54	0.23	**0.02**
Forest type CLEARCUT	1.11	0.34	**<0.01**	0.90	0.25	**<0.01**
Aspect NORTH	0.58	0.18	**<0.01**	1.45	0.18	**<0.01**
Trans. time AUTUMN	1.24	0.19	**<0.01**	1.24	0.17	**<0.01**
Survey year:Forest type	−2.80	0.52	**<0.01**	0.54	0.48	0.26
Survey year:Aspect	−1.25	0.36	**<0.01**	0.78	0.42	0.07
Forest type:Aspect	0.76	0.36	**0.04**	3.11	0.35	**<0.01**
Survey year:Trans. time	0.59	0.36	0.10	1.72	0.41	**<0.01**
Forest type:Trans. time				1.50	0.33	**<0.01**
Survey year:Forest type:Aspect	−3.69	0.72	**<0.01**	2.39	0.87	**0.01**
Survey year:Forest type:Trans. time				2.25	0.85	**0.01**

3.5. Control transplantation at collection site

Seventeen (85%) of the trees were still standing in 2008. The survival was in 2008 similar between fresh material (77% of transplants survived) and frozen (71%), and vitality of the survived transplants was also similar (77% were vital, for frozen as well as fresh material).

3.6. Comparison between survey years 1996 and 2008

The significantly higher survival in 2008 on northern sides of clearcut trees compared to southern sides or on forest trees was not seen in the 1996 data (Fig. 1 and Tables 2 and 3). The overall higher transplant vitality on northern sides compared to southern sides in 2008 (Fig. 2 and Tables 2 and 3) also differed from 1996 when there was a significant difference between clearcuts and forests with vitality being significantly higher on northern sides in clearcuts but not in forests (Fig. 2 and Table 2).

There was agreement between years in that there was no difference for transplant survival and vitality between grouped and scattered retention trees. Also, the survival of autumn transplants was in both survey years significantly higher than the survival of spring transplants. However, transplant vitality differed significantly between survey years with autumn transplants being significantly more vital in clearcuts in 1996 but showing no significant difference in 2008 (Tables 2 and 3).

4. Discussion

4.1. Retention trees as habitat for L. pulmonaria

The most important conclusion from our 14-year old transplantation experiment is that transplants of *L. pulmonaria* survived better on retained aspens on clearcuts than on forest trees, indicating that aspens left at clearcutting represent a suitable habitat for this species. The positive effect of retention trees was especially high on northern sides of tree stems, and thus microhabitat conditions seem decisive for species survival. Also transplant vitality was higher on northern sides of tree stems, but this did not differ significantly between retention trees and forest trees, indicating that some factor seriously affects transplant survival in the forests. One possible explanation might be gastropod grazing which has been increasingly noticed as an ecological driver of epiphytic population occurrences (e.g. Asplund et al., 2010). For *L. pulmonaria,* a positive correlation has been found between gastropod abundance and grazing damage (Vatne et al., 2010), and snails in the boreal zone are known to be promoted by aspen since the litter of this tree species has a relatively high pH (Karlin, 1961). It is likely that the grazing pressure is lower on clearcuts than in forests, since many snails are sensitive to disturbance and microclimatic changes (Hylander, 2011).

The higher survival on retained trees is unexpected since *L. pulmonaria* is most common in old-growth forest (Gärdenfors, 2010), i.e. the response of transplants does not match the actual occurrence pattern. However, large differences have been observed between potential and actual niches in lichen transplant studies. For instance, Sillett et al. (2000) found that transplants of *L. pulmonaria* were tolerant to open habitat conditions one year after transplantation, and Gauslaa et al. (2006) found *L. pulmonaria* transplants to have larger biomass growth in clearcuts than in old forests. Gauslaa et al. (2006) describe the long-term persistence of this species as a balance between light availability, where high levels benefit growth, and desiccation risk, since drought can drastically decrease populations. The relatively shady north side of retention trees is intermediate between the sun-exposed south sides of retention trees and the often very dark spots in old forests, and thus seems a favorable environment for *L. pulmonaria*. Our results agree with those of Hedenås and Hedström (2007) who found three macrolichens to be equally or even more abundant on aspens retained on clearcuts compared to forests, after 24 years.

Our study addresses the ability of already established thalli of *L. pulmonaria* to survive and stay vital on trees retained at harvest ("life-boating"), i.e. dispersal aspects were not in focus. Nevertheless, colonization of new trees will be decisive for the species' long-term persistence and thus is an essential aspect to investigate. Experiments with diaspores of *L. pulmonaria* (Scheidegger et al., 1995; Hilmo et al., 2011) indicate that establishment, contrary to survival and growth, is hampered by light-exposed conditions, and establishment constraints in young forests have also been suggested by Gjerde et al. (2012). Further studies are needed to examine if habitat requirements indeed differ for different life-history stages in *L. pulmonaria* and other lichens.

It might be surprising that no difference could be detected in either survival or vitality between transplants on aspens in groups and on scattered trees since tree groups could be expected to provide more semi-open conditions, beneficial to the lichen. But, a tree group according to our criteria did not have to consist of more than four trees which means that the groups could be very small, and thus the difference to scattered trees was not pronounced. Further, several trees in groups had fallen at the inventory after 14 years, and a young forest stand had developed, leveling out differences in the environment surrounding scattered aspens and aspens in groups.

Lack of natural young forests following fires in today's European boreal forest landscapes could mask important occurrence patterns of species that today are viewed as confined to high forest ages; the few remaining intact forests are all old-growth. Recent research indicates that stand-replacing fires were less common and fire frequencies and intensities lower than earlier thought in N. Europe, implying that there were usually numerous remnant trees in forests regenerating after fire (Kuuluvainen, 2009). It might be that such trees were important habitats for *L. pulmonaria* and other lichens. Thus, it can be discussed whether *L. pulmonaria* is a true old-growth lichen or if it is an old-growth species in the current N. European forest landscapes since natural early-growth forests are lacking. Only in the so far unlogged forest landscapes of N. Russia in which natural fire dynamics still remain would it be possible to study the association of *L. pulmonaria* and other epiphytic lichens described as sensitive, to different successional stages after natural disturbance. The importance to biodiversity of old-growth structures in early successional stages is today increasingly highlighted in ecology and conservation (Kouki et al., 2004; Swanson et al., 2011).

4.2. Correspondence in response patterns between inventories two years and 14 years after transplantation

Agreements between survey years in response of the transplants were overall large; survival was as high or higher on clearcut trees as on forest trees, and vitality was similar between clearcut and forest trees. The most important difference was the positive influence for survival of north sides of retention trees on clearcuts which had become evident after 14 years, indicating that the advantage of this microhabitat increases with time. Another difference was a significantly lower vitality for spring transplants than autumn transplants two years after transplantation but not after 14 years. Spring was unusually dry in the transplantation year, which evidently had a strong negative effect on the vitality of transplants mounted that season. But, the initial climatic differences may have been evened out during the following 12 years.

In the current study we used generalized linear mixed models as a statistical tool in order to explain survival and vitality in *L. pulmonaria* transplants. This approach was chosen since we wanted to account for the random effects of study sites and trees, and hence to avoid pseudoreplication. Our results on transplant survival and vitality after two years differed slightly from the data analysis presented in Hazell and Gustafsson (1999), since they used ordinal logistic regression and a different set of explanatory variables (that were not measured in 2008). One example is the significantly higher vitality on the south side of forest aspens demonstrated for the 1996 data with logistic regression of Hazell and Gustafsson but not with the GLMM used by us. Another is the significantly lower vitality shown for lichen transplants on scattered trees compared with trees in groups on clearcuts after two years using logistic regression, but not detected when using the GLMM on the same data. However, we believe that the GLMMs used here are more reliable since random factors were accounted for.

4.3. Management implications

Our study shows that retention of aspens at clearcutting can be of importance to the lichen *L. pulmonaria*, and most likely also to other lichen species with similar habitat demands in the boreal zone. If not all aspens can be retained, such with *L. pulmonaria* should be prioritized, because it is an uncommon, red-listed species, and highest priority should be given to trees where it occurs on the north side. There are signs of continued decline in *L. pulmonaria* in Sweden (Fritz, 2011) and if it reaches very low population levels, one alternative could be translocation of the species to new sites. Our study indicates that in order for this to be efficient, northern sides of trees are preferable, and a careful selection of transplantation occasion in periods of high precipitation and humidity is advantageous.

Maintaining and also increasing the amount of old aspens and also other host tree species in heterogeneous forest landscapes will be a prerequisite for continued survival of *L. pulmonaria* in boreal N. Europe. The relatively new practice of retaining trees at harvest, in which aspens are prioritized, is a key action to secure persistence of this important habitat. Another important measure is to leave aspens during pre-commercial and commercial thinnings, to guarantee a continuous supply of aspens of different sizes and ages over time.

The higher transplant survival on aspens on northern sides of trees in clearcuts than in forests indicate that the species is promoted by semi-open conditions with moderate light levels, which benefit growth but are not strong enough to cause fatal damage (Gauslaa et al., 2006). Many old forests with aspens in Fennoscandia are today darker and denser than before, when there were more fires and cattle grazing. For several decades there has been vigorous in-growth of *P. abies* in these forests, creating a dark climate which is likely negative for *L. pulmonaria.* Thinning and selective felling of spruce is an efficient method to create more favorable conditions for this species and other lichens of the *Lobarion* community. The preference for rather open canopies in boreal forests is also shared by other rare lichen species like the long-beard lichen *Usnea longissima* Ach. (Josefsson et al., 2005).

5. Conclusions

Our transplantation experiment shows that aspens retained at final harvest provide good habitat for *L. pulmonaria* and thus that leaving aspens unlogged is an efficient conservation measure. Transplantation of lichens is an informative method to address conservation biology questions related to epiphytes and can yield valuable insights already after short time spans. However, long time-series are needed to identify more specific response patterns. Optimally, real occurrences should be followed over time, but in the case of *L. pulmonaria*, which is uncommon in Sweden today, finding large sample sizes is impossible if variation in forest ages and site conditions are to be controlled for. Still, extensive surveys of this lichen and the whole epiphytic lichen community connected to aspen in different forest ages would yield a deeper understanding necessary for development of more fine-tuned conservation recommendations.

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