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REGULAR PAPER

Effects of heathland management on seedling recruitment of common juniper (*Juniperus communis*)

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Background and aims – Common juniper (*Juniperus communis* L.) is one of the most widespread woody species on the planet. Over recent decades, however, common juniper populations are decreasing in size and number in different regions. Lack of recruitment, caused by extremely low seed viability and the absence of suitable microsites for recruitment, is the key reason for this decline. For successful germination, the seeds need gaps in the existing vegetation and a soil with a relatively high base saturation. The aim of this study was therefore to assess how management actions such as sod cutting, rotavation and liming (alone or in various combinations) influence soil characteristics, seed germination and seedling survival of common juniper.
Methods – We installed a sowing experiment across 104 1-m^2 plots in four different sites in Belgium and the Netherlands using treatments with different combinations of fencing, sod cutting, rotavation, litter addition and liming. We determined how these treatments affected soil characteristics and how they influenced seed germination and seedling survival.
Key results and conclusions – Across the whole experiment, germination rates of juniper seeds were very low (almost always < 1%). Our results confirm that bare ground promotes the germination of juniper seeds. Secondly, higher silt and lutum (clay) proportions in the soil and higher soil organic matter content seemed to have a positive impact on recruitment, possibly due to drought reduction. Management actions that negatively affect those soil characteristics, such as deep sod cutting, should thus be avoided in heathlands on sandy soils. Our results reveal a complex relationship between seedling recruitment success, soil conditions and management of common juniper populations. Overall, combinations of fencing, (superficial) sod cutting and liming or rotavation were most successful.

Keywords – *Juniperus communis*; germination; seedling survival; sod cutting; rotavation; liming; heathland.

INTRODUCTION

With a distribution range that covers most of the northern hemisphere (Adams 2008), common juniper *Juniperus communis* L. (further referred to as '(common) juniper') is one of most widespread plant species on earth. In the last decades, however, multiple studies are reporting declining size and number of juniper populations in different regions, including the northwestern European lowlands (e.g., the Netherlands: Oostermeijer & De Knegt 2004; England: Clifton et al. 1997) and the Mediterranean mountain regions (García et al. 1999). Although the species can locally still be very abundant and

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exhibit good regeneration (e.g., in the Alps, Scandinavia and Poland; Falinski 1980; Rosén 1995; Rosén & Baker 2005), common juniper communities are listed in Annex I of the EU Habitat Directive (code 5130) due to their threatened status in several European regions.

Together with European yew (*Taxus baccata*) and Scots pine (*Pinus sylvestris*), juniper is one of the only three native conifers in Belgium and the Netherlands. In these regions, the species mainly occurs on nutrient poor, acid, sandy soils, typical for heaths and drift sands. Due to land-use changes related to afforestation, agriculture and urbanisation, the area of heathland and drift sands has largely declined in the 20th century (Webb 2002; Piessens et al. 2004, 2005). In addition, increased atmospheric deposition of nitrogen and sulphur compounds has caused soil acidification in the remaining heathlands and disturbance of the nutrient balance (Bobbink et al. 1992). Despite efforts during recent decades for stopping habitat destruction and degradation, the decline of juniper is still ongoing in these habitats, mainly because of a lack of recruitment (e.g., Verheyen et al. 2009). Verheyen et al. (2009) revealed a triangular relationship between the fraction of recently recruited individuals and the percentage of viable seeds in a population. This means that if seed viability is low, recruitment is negligible, while in case of a high percentage of viable seeds other factors such as herbivory, summer drought and the absence of suitable microsites for germination are responsible for the differences in recruitment between populations. Thus, the lack of recruitment is not only due to low seed viability (Ward 1973, 1982; Fitter & Jennings 1975; Gilbert 1980; García 2001; Broome et al. 2017).

For successful recruitment, the seeds need gaps in the existing vegetation and a soil with a relatively high base saturation degree. In addition, seeds should be covered by a thin layer of soil, stay relatively moist and be located in open habitats, free from shading by vegetation (McVean 1966; Livingston 1972; Ward 1973; Fitter & Jennings 1975; Clifton et al. 1997; Hommel et al. 2009). Although grazing by e.g., sheep and cattle can help to achieve these conditions (e.g., Fitter & Jennings 1975; Hommel et al. 2009; Broome et al. 2017), this type of management also risks eliminating new seedlings and damaging mature shrubs by grazing (Ward 1973; Clifton et al. 1997; Broome et al. 2017). Taking this risk into account and the already threatened status of the remaining juniper populations in Belgium and the Netherlands, there is a need for other management types to obtain suitable microsites for germination.

Removal of organic material by sod cutting such that gaps are created and competition of other plants is reduced is an oft-used management technique to maintain oligotrophic systems such as heathlands (Aerts & Heil 1993). However, due to the ongoing acidification of heathlands in Belgium and the Netherlands, the soil pH is shifting towards the aluminium and iron buffer range which can result in elevated soil Al^{3+} availability (pH < 4.5; Bowman et al. 2008). High soil Al^{3+} concentrations can be toxic for plants and prevent germination of seeds (Ulrich & Sumner 1991; van den Berg et al. 2003). The toxicity of Al^{3+} can be reduced if the Al^{3+} is complexed with organic compounds (Ulrich & Sumner 1991). However, through sod cutting, the organic matter concentration in the soil and the reduction potential of Al^{3+} may decrease. Additional liming to move the soil in the cation exchange buffer range ($4.5 < pH(H_2O) < 8$; Bowman et al. 2008) can therefore be useful (van den Berg et al. 2003; Dorland et al. 2004). Finally, rotavation, i.e., mechanically breaking up the soil (sometimes referred to as scarification), can also create bare ground. Since pronounced vertical pH gradients can exist in sandy heathland soils (acidic top layer, less acidic below; De Bakker 1979), rotavation and soil mixing can also increase topsoil pH. However, this management can negatively influence other species as their seed banks can become buried too deeply.

Although the abovementioned management actions have the potential to ameliorate the conditions for germination and seedling survival of juniper, the actual effects and their mechanisms are still not known. Here we experimentally assessed how management actions in heathlands including sod cutting, rotavation, and liming (alone or in various combinations) influence soil characteristics suitable for juniper regeneration from seed. We studied the effects of the different management actions in heathlands on seedling recruitment (seed germination and seedling survival) of common juniper.

METHODS

Study species

Common juniper is a dioecious, wind-pollinated shrub or tree and the female specimens annually produce fleshy, spherical, berry-like cones of approximately 6 mm in diameter that take two or three years to ripen (Ottley 1909; García et al. 2000; Thomas et al. 2007; Ward 2010). The sexual reproduction starts with the cone initiation in autumn or early winter (Singh 1978) with the female strobili usually containing three ovules (Thomas et al. 2007). In a two year-cycle, pollination takes place in next spring and fertilization follows in the summer of the same year. After fertilization, the embryo development starts and by the end of the summer of the second year the seeds are ready for dispersal. In a three-year cycle, the fertilization is postponed with one year and takes place in the summer of the second year such that seeds are ripe for dispersal by the end of the summer of the third year (Ottley 1909; García et al. 2000; Thomas et al. 2007; Ward 2010; Gruwez et al. 2012). A detailed description of the seed and cone development is available in Gruwez et al. (2012). Seeds that are ready for dispersal have a dormant embryo and need to undergo an after ripening-process before they can germinate (Pack 1921). Different treatments to improve germination have been tested (e.g., Pack 1921; McVean 1966; Broome 2003; Adriaenssens et al. 2006) with variable success. However, good results in breaking dormancy were achieved if the seeds are stored at temperatures between 0 and 10°C with an optimum of 4–5°C (Pack 1921; McVean 1966; Broome 2003). Pack (1921) found that storage in cold (-23°C) and moist conditions or in conditions of altering temperatures negatively affected germination. McVean (1966) and Broome (2003) advise the use of cleaned seeds, but Adriaenssens et al. (2006) reported good germination results when cones were sown.

Experimental design

Two similar, but slightly different, experiments to examine the influence of management treatments on the seedling recruitment of common juniper were conducted in Belgium and the Netherlands.

Belgium – In Belgium, the experiment was installed during the winter of 2008–2009, two months before sowing. We installed 48 1 × 1 m experimental plots at two different sites in the Campine region (24 plots on each site): one at the Mechelse Heide (51.0°N, 5.6°E, 95 m a.s.l) and one at the Ten Haagdoorn Heide (51.0°N, 5.4°E, 72 m a.s.l.). Both sites are dry heathlands on a poor, loamy (11.3% loam at Mechelse Heide and 9.0% at Ten Haagdoorn Heide) sandy soil dominated by *Calluna vulgaris* shrubs of approximately 0.5 m high. At each site, six treatments were applied (4 replicates per treatment and per site):

(1) control (no treatment (C));

(2) fencing (F);

(3) fencing + deep sod cutting (F+S);

(4) fencing + deep sod cutting + lime addition (F+S+L);

(5) fencing + deep sod cutting + rotavation (F+S+R);

(6) fencing + deep sod cutting + lime addition + rotavation (F+S+R+L).

Fencing (1.5 m high, 0.05 m mesh width, and 20 cm depth in the soil) excluded small (e.g., rabbits) and large (e.g., roe deer) mammalian herbivores. In the sod cutting treatment, we removed the organic layer while in the 'rotavation' treatment, the soil was turned over and mixed to a depth of 30 cm. In the lime addition treatment, 2000 kg ha^{-1} dolomitic lime (48% CaO + MgO; 33% CaO; 15% MgO; max. 6 mm granules) was added to the plots.

We used seeds of four different provenances to also determine the effects of seed origin and seed viability. To be able to study which treatments led to the most successful recruitment, we also used seed origins with likely higher germination rates. We are aware that – by using seed material from other regions than the study sites – we are introducing genetic material that is possibly not perfectly adapted to local conditions. However, Vanden Broeck et al. (2011) showed that the genetic diversity both between and within populations in northwestern Europe is still high, thereby probably making the origin of the mother plants less important (see also Gruwez et al. 2014). If only seeds from Flanders (As, Mechelse Heide population), with an extremely low seed viability, would have been used, the chance of success of this experiment would be extremely low. In addition, young shrubs have a higher seed viability (Gruwez et al. 2014). In Flanders, reintroduction programmes with young shrubs are being performed. We therefore sampled seeds in Belgium (As, Mechelse Heide, 51.0°N, 5.6°E), but also in populations from regions in Europe where seed viability is still relatively high: Ekulunde (56.6°N, 16.6°E) in Sweden, Kleszczele (52.6°N, 23.3°E) in Poland, and Rossdach (50.0°N, 11.1°E) in Germany (see Gruwez et al. 2012 for more information on these juniper populations). During November and December of 2008, ripe cones were sampled in each of the populations on 10 to 15 randomly selected, cone-bearing shrubs until sufficient seeds for this experiment were sampled (assuming all parent trees and all parts of the crown of the parent tree contribute equally to the whole seed sample such that this source of variation was randomly distributed across the treatments). During the winter of 2008–2009, the cones were stored outdoors, shaded and dry in open plastic pots. Every plot was divided into four subplots of 0.4 × 0.4 m. In early February 2009, we sowed the cones in these subplots (25, 20, 30 and 30 cones per subplot for the Ekulunde, Kleszczele, Rossdach and As populations, respectively) and, where sod cutting was applied, covered them with a thin layer of soil. We also avoided sowing seeds in a buffer zone of 0.1 m around each subplot to exclude edge effects. Germination and survival of the seedlings was recorded in September 2009, 2010 and 2011. For each population, the average number of seeds per cone and the percentage of potentially viable seeds was determined by opening a subset of 50 cones per population, counting the seeds in the cones and cutting the seeds. If the embryo and megagametophyte were white and smooth, the seeds were considered as potentially viable (see Gruwez et al. 2012 for a detailed account of the methods).

The Netherlands – In the Netherlands, a similar experiment was performed at two locations: Mantinge (52.8°N, 6.6°E, 50 m a.s.l.) and Markelo (52.3°N, 6.5°E, 50 m a.s.l.). The soil of the first site developed in drift sand and has a very low loam content (1%). The second location has a soil that developed in sand with a loam content of c. 7%. Each experimental site existed of 28 plots of 1.5 × 1.5 m of which the central part (1 × 1 m) was used to sow the seeds and the exterior for the soil sampling. Seven different treatments were applied to the plots:

(1) fencing (F);

(2) fencing + shallow sod cutting (F+S1);

(3) fencing + deep sod cutting (F+S2);

(4) fencing + deep sod cutting + litter addition (F+S2+Li);

(5) fencing + deep sod cutting + rotavation (F+S2+R);

(6) no fence + deep sod cutting + lime addition (S2+L);

(7) fencing + deep sod cutting + lime addition (F+S2+L).

In the shallow sod cutting treatment, the sod was removed to a depth of c. 2 cm, while in the deep sod cutting treatment the sod and part of the mineral soil rich in organic matter to a depth of c. 5 cm was taken away. In plots with litter addition, a layer of 5-cm thick common juniper litter was spread over the plot. Similar to the Belgian experiment, rotavation turned over and mixed the soil to a depth of 30 cm. Liming was performed by spreading 2000 kg ha^{-1} dolomitic lime (84% $CaCO_3$; 10% $MgCO_3$). The fencing again excluded herbivores such as rabbits and roe deer (same type of fences as in Belgium). The plots were divided in two equally-sized subplots. In the first subplot, c. 1000 cones per subplot were sown between February and March 2008. The cones were sampled in the autumn and winter of 2006–2007 in three areas in the Netherlands: Dwingelderveld (52.8°N, 6.4°E), Mantinge (52.8°N, 6.6°E) and Junner Koeland (52.5°N, 6.5°E). The average number of seeds per cone and the percentage viable seeds were estimated using the data of the Dutch populations sampled by Gruwez et al. (2012). In the second half of the subplots, c. 800 cones per subplot were sown in March 2009. These cones were sampled in November 2008 in a common juniper population, Buinen (52.9°N, 6.8°E) in the Netherlands, which still exhibits high levels of recruitment (up to 70 seedlings/m^2). Similarly to the Belgian experiment, a subsample of 50 cones was used to estimate the number of seeds per cone and seed viability.

During both sowing events the cones were placed in four rows and covered with c. 0.5 cm sand, except in the reference plots (F), where the cones were sown randomly and not covered. Germination and survival of the seedlings was recorded in the spring, summer and autumn of 2008 and 2009, in the summer and autumn of 2010 and in the autumn of 2011. Movement of the cones, caused by wind and rain, made it difficult to determine with certainty whether a seedling was originating from seed of the first or the second sowing event. Therefore, we analysed germination and seedling survival of the two subplots together and used the average of both sowing events for the number of seeds per cone and seed viability.

Soil sampling and analysis

In each subplot of the Belgian experiment, 4 soil samples (0–10 cm) were collected during the winter of 2011–2012, pooled per plot, dried at 40°C for 48 h, and sieved through a 1-mm sieve. In the plots where there was no sod cutting, the litter layer was removed before soil samples were taken. The soil pH-KCl of each sample was analysed using a glass electrode (Orion, Orion Europe, Cambridge, England, model 920A) after extracting 14 mL soil in 70 mL KCl (1 M) solution. The percentage of silt + lutum (clay) in the soil was estimated using procedures of the Dutch Soil Survey Institute (Soil Survey Staff 1975). Soil organic matter was estimated by loss on ignition (four hours at increasing temperature until 450°C) as soil organic matter = 100 - % of ashes residue. Total phosphorus (P) was colourimetrically analysed following the method of Scheel (1936). NH_4^+ acetate-EDTA extractable K^+, Mg^{2+}, Ca^{2+} and Al^{3+} concentrations were analysed by atomic absorption spectrophotometry (AA220, Agilent Technologies Belgium, Diegem, Belgium) after shaking 10 g of dry soil in 50 mL NH_4^+ acetate-EDTA solution (192.5 g NH_4^+ acetate, 50 mL acetic acid, and 29.225 g EDTA, diluted to 2 L) for 30 min.

In the Netherlands, in each plot the humus layer was described and four soil samples (0–10 cm) were collected, pooled, air dried and sieved through a 0.5 mm mesh. If present, the litter layer was removed before sampling. Moisture was determined after drying the sieved samples at 105°C for 4 h. We determined pH-KCl and the percentage of silt + lutum in the soil similarly as for the sites in Belgium. Soil organic matter was estimated by loss on ignition (at 380°C) as soil organic matter = 100 - % of ashes residue. Total phosphorus (P) was analysed using a Kjeldahl destruction. Exchangeable Ca^{2+}, Mg^{2+}, K^+ and Na^+ was analysed by atomic absorption spectrophotometry after a Bascomb extraction at pH = 8.1 (Bascomb 1964).

Data analysis

Our analyses were performed for both countries separately due to the slightly different design and followed the following two steps: quantify the effects of (i) the experimental treatments on soil characteristics, and (ii) all the soil management treatments on germination and survival of juniper seeds and seedlings. All analyses were performed in R version 3.6.2 (R Core Team 2019).

First, to calculate the effects of the different treatments on soil characteristics, we applied linear mixed-effects models with the lmer-function of the lme4-package were applied and site of the experiment (Mechelse Heide or Ten Haagdoorn Heide, Mantinge or Markelo) was added as a random-effect term. To fulfil normality and homoscedasticity assumptions, logarithmic transformations were performed on the soil organic matter, silt + lutum content, pH, P, Mg^{2+}, Ca^{2+} and Al^{3+} for the Belgian experiment and on the soil organic matter, silt + lutum content, Mg^{2+} and Ca^{2+} for the Dutch experiment.

In the second step, we quantified the effects of the experimental treatments directly on germination and survival. The Belgian and Dutch data were again analysed separately. The effects of the soil treatments on the proportion of germinated seeds as well as the proportion of seedlings that survived till the end of 2011 were analysed by fitting Bayesian Generalised Linear Mixed Models using Markov chain Monte Carlo techniques with binomial data using the MCMCglmm-function with the family 'multinomial2' in the MCMCglmm-package (Hadfield 2010). To account for the hierarchical design, the location of the experiment (and the provenance of the seeds for the Belgian experiment only) was used as random-effect term. We used 100,000 iterations after a burnin of 5,000, ran three independent chains to check for model convergence and used the default priors of the MCMCglmm package.

We also analysed our data using principal components analysis (PCA) of the soil variables and the percentage of germinated seeds at the plot level using the prcomp-function in R. These results are displayed in supplementary file 1.

RESULTS

Germination rates vs. origin

We counted only 176 seedlings for c. 260,491 sown seeds across both countries. Thus, average germination rates were extremely low, especially for seeds that originated from Belgium and the Netherlands (table 1). The Belgian seeds displayed extremely low seed viability. The Rossdach population (Germany) delivered the most viable seeds. Absolute germination rates differed by a factor of around 50, while germination rates of the viable seeds were less different among the origins (17-fold). Germination rates of the viable seeds in the Dutch experiments were still very low.

Soil characteristics vs. treatments

In Belgium, the effects of liming (treatments F+S+L and F+S+R+L) on the soil were very clear for pH and the concentrations of Mg^{2+}, Ca^{2+} and Al^{3+} (table 2, fig. 1). In both treatments pH, Mg^{2+} concentration and Ca^{2+} concentration were significantly higher than in the control plots and Al^{3+} concentrations were significantly lower (table 2). Total P-

Table 1 – Information on the seeds used in the experiment.
The number of sown seeds, their viability and the percentage of germinated seeds per origin. *These data were estimated based on the Dutch populations in Gruwez et al. (2012).

Origin	Number of cones sown	Average seeds per cone	Number of sown seeds	Percentage viable seeds (%)	Number of seedlings across all plots	Percentage seeds germinated (%)	Percentage viable seeds germinated (%)
Ekulunde (Sweden)	1200	2.91	3492	3.87	7	0.20	5.18
Kleszczele (Poland)	960	2.57	2468	4.32	18	0.73	16.89
Rossdach (Germany)	1440	2.62	3773	26.62	66	1.75	6.57
As (Belgium)	1440	2.58	3715	0.65	2	0.05	8.28
The Netherlands	86400	2.86*	247044	3.35*	83	0.03	1.00

content was significantly lower in all treatments where sod cutting took place (table 2).

The Dutch experiment showed a significant increase in pH in all treatments (table 2) except for the plots where only shallow sod cutting (F+S1) took place. Soil organic matter strongly decreased in treatments with deep sod cutting and also in the treatment with deep sod cutting and litter addition. Mg^{2+} and Ca^{2+} concentrations were significantly lower in plots with treatment F+S2+R and with treatment F+S2 and higher in the plots with treatment S2+L (table 2). The percentage silt + lutum was remarkably lower in Mantinge and in treatments F+S2, S2+L and F+S2+L (table 2) compared to the control (F). The total P content was significantly lower in all treatments where sod cutting took place except for the rotavation plots (table 2).

Germination and survival

We found overall higher germination at sites with higher soil organic matter and higher silt + lutum content (fig. 2). In three of the four sites, no seeds germinated where no sod cutting took place (fig. 2). The Mantinge site also experienced extremely low germination rates, which is likely due to the low loam percentage in that area (c. 1%) in comparison to the other sites (7–15.7%). In Belgium, fencing + sod cutting + liming was most successful, followed by fencing + sod cutting, and it were the only treatments that resulted in significantly more seedlings than the control (table 3). In the Dutch experiment, no seeds germinated in the control (fenced) plots (F) and two treatments (F+ S2+R and F+S2+L) were the most successful (highest posterior mean in table 3). All four other treatments (F+S2 and S2+L first, followed by F+S1 and F+S2+Li) were also significantly better than the control (table 3). Mortality did not depend on the treatment in the Belgian experiment, but the F+S1 treatment had the lowest mortality in the Netherlands (fig. 2).

DISCUSSION

The main goal of our research was to assess the effects of heathland management on germination and seedling establishment of common juniper on sandy soils. Second, we aimed to explain seedling recruitment patterns by changing soil conditions under the different management practices. Deep sod cutting in combination with liming or rotavation were the most successful in improving seedling recruitment in common juniper. This effect can mainly be explained by the creation of bare soil. Effects of pH and the amelioration of the base saturation degree, however, seemed to be induced by the contrasting soil conditions between the sites and by liming. In addition, drought stress emerged as a plausible important factor for germination. We first discuss the differences in seed viability and germination success between the origins of the seeds and between the experimental sites. Second, we explain the different germination rates depending on treatment and soil condition. Finally, the challenges for common juniper management and practical advice concerning the creation of suitable conditions for juniper recruitment in heathlands are summarized.

Seed viability of common juniper in Belgium and the Netherlands is extremely low. Unsurprisingly, seeds that originated from populations with relatively high percentages of viable seeds (e.g., those from Germany) had the best absolute germination success. This is in accordance with the findings of Verheyen et al. (2009) who revealed a triangular relationship between seed viability and the percentage recruitment in a population. However, germination rates were still very low (generally below 1% and with a max of 1.75%), regardless of the origin and percentage of viable seeds, which suggests that there are additional causes for failing germination. In the Dutch experiment, germination rates were exceptionally low (0.03%) and this is not uncommon (Gruwez et al. 2014; Broome et al. 2017). The sites and soil treatments were more or less comparable between the two experiments, thus probably other variables such as drought stress and herbivory were responsible for these differences.

Our results corroborate the necessity of bare soil for germination of common juniper seeds (Ward 1973; Clifton et al. 1997; Hommel et al. 2009; reviewed in Broome et al. 2017). Little or no seeds germinated on the plots without sod cutting, except in the Mechelse Heide in Belgium, where the organic layer was rather thin. This result is further corroborated by the plots where litter of common juniper was added: seedlings could only establish in places where the litter had already decomposed.

Table 2 – Soil variables in the different treatments compared to the control.
The direction of the arrows indicates a higher (↑) or lower (↓) value in the treatment than in the control. The number of arrows reflect the significance of the statistical test. The total number of plots was n = 48 in Belgium and n = 56 in the Netherlands. n.s.: not significant, ↓ or ↑: $p < 0.05$, ↓↓ or ↑↑: $p < 0.01$, ↓↓↓ or ↑↑↑: $p < 0.001$. F: fencing; S: deep sod cutting in Belgium; S1: shallow sod cutting in the Netherlands; S2: deep sod cutting in the Netherlands; L: liming; R: rotavation; Li: addition of common juniper litter; OM: soil organic matter. All variables were log-transformed prior to the analyses except soil pH in the Netherlands.

Country	Treatment	Soil variables						
		OM	silt + lutum	pH	P	Mg^{2+}	Ca^{2+}	Al^{3+}
Belgium	F	n.s.	n.s.	n.s.	n.s.	n.s.	↑↑	n.s.
	F+S	↓	n.s.	n.s.	↓↓↓	n.s.	n.s.	n.s.
	F+S+L	↓	n.s.	↑↑↑	↓↓	↑↑↑	↑↑↑	↓↓↓
	F+S+R	↓	n.s.	n.s.	↓↓↓	n.s.	n.s.	n.s.
	F+S+R+L	n.s.	n.s.	↑↑↑	↓↓	↑↑↑	↑↑↑	↓↓↓
The Netherlands	F+S1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
	F+S2	↓↓↓	↓↓	↑↑↑	↓	↓↓↓	↓↓↓	
	F+S2+Li	↓↓↓	n.s.	↑↑↑	↓↓	n.s.	n.s.	
	F+S2+R	n.s.	n.s.	↑↑↑	n.s.	↓	↓	
	S2+L	↓↓↓	↓↓	↑↑↑	↓↓	↑↑	↑	
	F+S2+L	↓↓↓	↓	↑↑↑	↓	n.s.	n.s.	

Second, an extremely low silt + lutum proportion in the soil and low soil organic matter content seemed to have a negative impact on germination: especially after deep sod cutting the remaining organic matter in the soil must be sufficiently high. This is highlighted by the low germination rates and low silt + lutum and organic matter contents of the soil in the Mantinge vs. other sites. Thus, the most important factor that results in variation in the silt + lutum content was the site, but also the experimental treatments affected this (table 2). For instance, the treatment that included sod cutting in Mantinge led to relative high soil organic matter and silt + lutum contents. These findings suggest that drought stress could be an important factor in the failing germination of common juniper seeds (see also Rosén 1988; Broome et al. 2017), as both soil organic matter (Stevenson & Cole 1999) and silt + lutum (Fitter & Hay 2002) content are responsible for elevated water availability in the soil. Average silt + lutum concentrations were at least 2.6% higher in the Belgian sites than in the most successful Dutch site (Markelo). As the nutrient concentrations and pH of the soils were comparable, it is likely that the large differences in germination rates can be explained by lower water availability, caused by a lower silt + lutum and/or soil organic matter content. To assess the role of drought stress on recruitment experimentally, for instance, experiments with rainout shelters could be the focus of future research. Carrer et al. (2019) recently also stressed the importance of winter precipitation for growth of juniper adults.

Although the presence of bare soil and drought stress seem to be important factors in the germination process, there is still variation in germination success between comparable plots related to these factors. For example, although sod cutting is effective for the creation of bare ground and the removal of excessive nutrients and competing vegetation (e.g., Niemeyer et al. 2007), this is not always sufficient to result in significantly higher germination rates (e.g., the Belgian experiment). A combination with management that increases the soil pH seems often necessary. The ongoing soil acidification of heathlands, a natural process on sandy soils that is accelerated due to the recalcitrant litter of heath vegetation and due to atmospheric deposition of mainly nitrogen (Roelofs 1986; Aerts et al. 1991; Uren et al. 1997), is associated with a decrease of exchangeable base cations and the increase of exchangeable soil Al^{3+} concentrations (Bowman et al. 2008). Also, in our study area, pH-KCl values of soils in the control plots were lower than 3.6 (i.e., a pH-H_2O of 4.4 after conversion *sensu* Azevedo et al. 2013) and soils were within the aluminium and iron buffer range (pH-H_2O < 4.5; Bowman et al. 2008). Thus, there is a risk of negative toxic effects of Al^{3+}, for example on plant roots, with typical symptoms as root length reduction, mortality of the root apical meristem and a reduction of Ca^{2+} and Mg^{2+} uptake (Runge & Rode 1991). Sod cutting down to the mineral soil can increase the pH due to the removal of the acidic top layer (Van Den Berg et al. 2003). This was most pronounced in the deep sod cut treatment in the Netherlands. However, pH values remained low, and, in Belgium, when not limed, pH values hardly reached the cation exchange buffer range (maximum soil pH-H_2O of 4.7). In addition, at low pH values, sod cutting can have a negative impact on germination as the removal of organic compounds reduces the capacity of complexing the toxic aluminium (Van den Berg et al. 2003) and acidification accelerates. We note, however, that we have only taken soil samples in one year (in the winter of 2011–2012) at the end of the experiment and, as such, some of the more dynamic soil characteristics (e.g., soil pH) could have changed over the course of the experiment; we cannot quantify this, however, with the data at hand.

Other studies therefore proposed additional liming after sod cutting to increase soil pH and base saturation (De

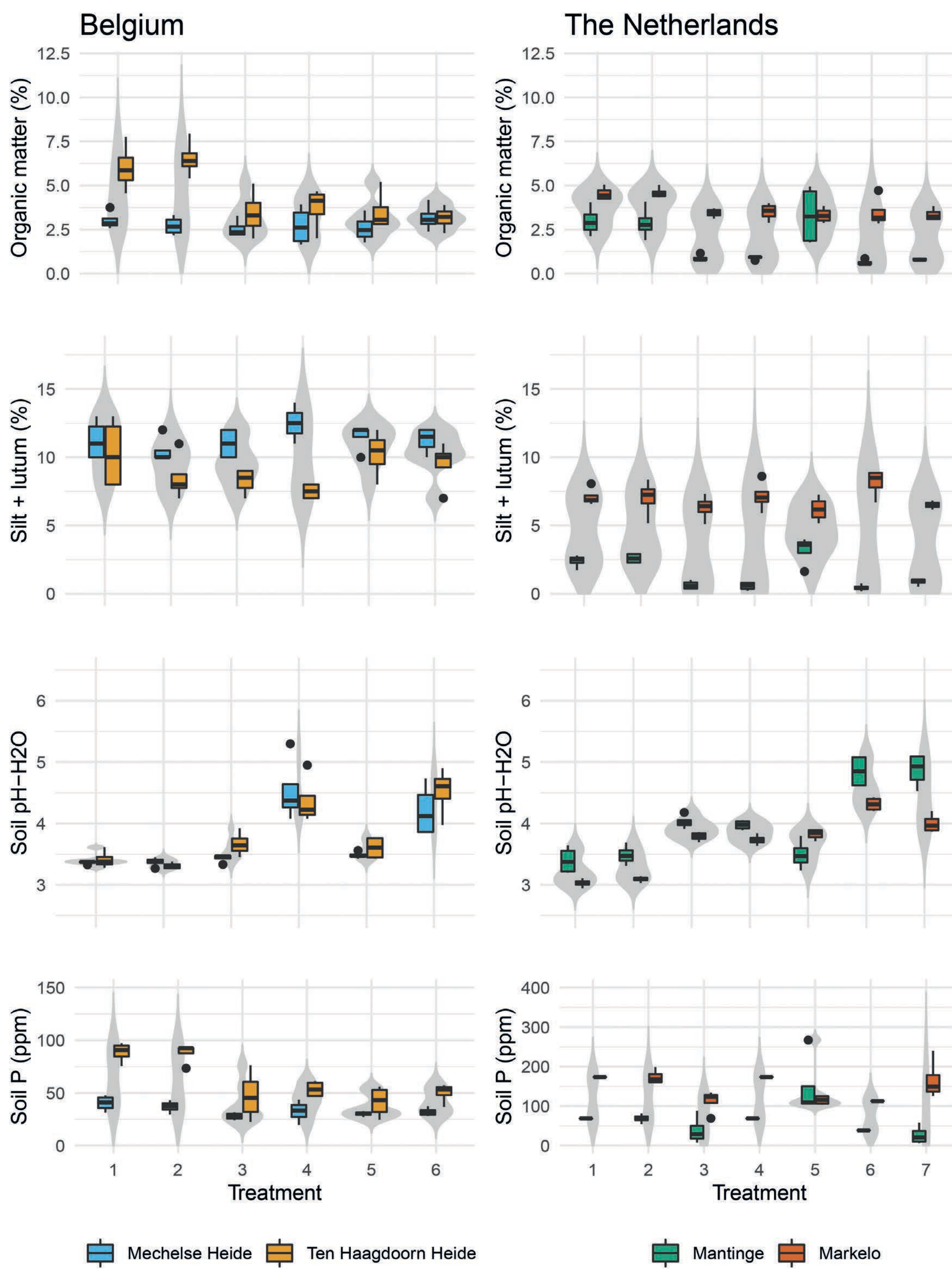

Figure 1 – The response of the soil characteristics to the experimental treatments. Treatments in Belgium were 1: control, 2: fencing, 3: fencing + deep sod cutting, 4: fencing + deep sod cutting + lime addition, 5: fencing + deep sod cutting + rotavation, 6: fencing + deep sod cutting + lime addition + rotavation. Treatments in the Netherlands were: 1: fencing, 2: fencing + shallow sod cutting, 3: fencing + deep sod cutting, 4: fencing + deep sod cutting + litter addition, 5: fencing + deep sod cutting + rotavation, 6: no fencing + deep sod cutting + lime addition, 7: fencing + deep sod cutting + lime addition. The total number of plots was n = 104; n = 48 in Belgium (24 per location) and n = 56 in the Netherlands (28 per location).

Graaf et al. 1998; Van den Berg et al. 2003). In our study, liming had a strong positive effect on the pH. In Belgium, liming was necessary to lead to better germination rates than in the control plots. However, in the Netherlands, there was no difference in germination success between the two other successful treatments without liming (F+S2 and F+S2+R). It is possible that the subtle higher pH after deep sod cutting in the Netherlands compared to the Belgian experiment can explain this effect. This means that in the Belgian experiment, extra liming was needed to sufficiently raise the pH. Surprisingly, rotavation in Belgium seemed to neutralize the influence of liming. Increase of pH and cation-concentrations were accompanied by a strong decrease of soil Al^{3+} concentrations in Belgium. These findings support the hypothesis of Al^{3+} toxicity inhibiting germination and seedling establishment of common juniper (also stressed by Lucassen et al. 2011). The treatment with both deep sod cutting and rotavation in the Netherlands (F+S2+R) increased soil pH. Probably this effect was generated by the combination of the removal of the acid top layer and the mixture with less acidic subsoil. A positive consequence is that the soil organic matter and silt + lutum content did not significantly decrease, probably due to mixture with organic matter from the deeper soil. Both soil organic matter and silt + lutum are important as they improve the buffering capacity of the soil. In other successful treatments, silt + lutum and/or soil organic matter content are lowered. Thus, it is possible that the positive effects of liming and deep sod cutting are not sustainable due to a lower capacity of the soil to retain a large amount of cations. In addition, if too much liming causes a high increase of the

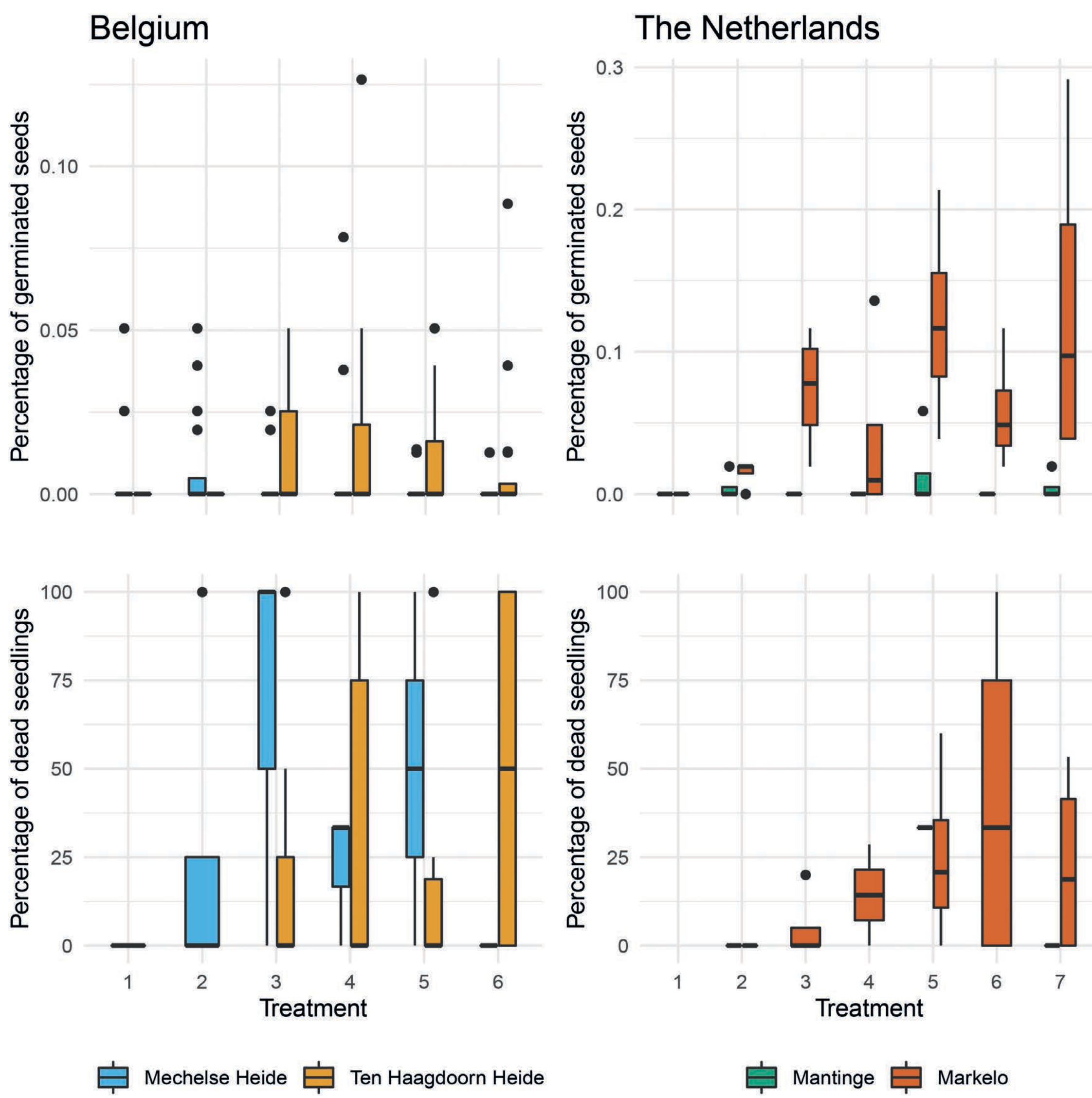

Figure 2 – The response of common juniper seed germination and seedling survival to the experimental treatments. The percentage of germinated seeds and dead seedlings and the different soil variables are displayed per treatment and per site as violin and box plots. The proportion of germinated seeds (and dead seedlings) was calculated by dividing the number of germinated seeds by the total number of germinated plus non-germinated seeds (and dead seedlings divided by the total number of living and dead seedlings, respectively). Treatment numbers are described in the caption of figure 1. The total number of plots was n = 104; n = 48 in Belgium (24 per location) and n = 56 in the Netherlands (28 per location).

Table 3 – **Germination and survival rates in the different experimental treatments, compared to the control plots.**
Because no seeds germinated in the control treatments (F) in the Netherlands, F+S1 was used as control comparison for survival. The number of replicate plots was n = 48 in Belgium (and n = 4 × 48 = 192 subplots) and n = 56 in the Netherlands. n.s.: not significant. F: fencing; S: deep sod cutting in Belgium; S1: shallow sod cutting in the Netherlands; S2: deep sod cutting in the Netherlands; L: liming; R: rotavation; Li: addition of litter.

Country	Treatment	Germination		Survival	
		Posterior mean with 95% CI	p-value	Posterior mean with 95% CI	p-value
Belgium	F	0.35 [-1.30, 1.99]	0.689	-236 [-562, 98.1]	0.166
	F+S	1.43 [-0.02, 3.04]	0.047	-264 [-568, 20.0]	0.074
	F+S+L	1.80 [0.27, 3.31]	0.008	-260 [-569, 27.4]	0.080
	F+S+R	1.18 [-0.32, 2.76]	0.112	-254 [-551, 60.0]	0.102
	F+S+R+L	0.67 [-0.87, 2.34]	0.392	-258 [-573, 42.4]	0.100
The Netherlands	F+S1	23.3 [0.61 , 68.1]	0.002	-	-
	F+S2	24.5 [2.02, 69.2]	< 0.001	-71.0 [-121, -0.69]	0.007
	F+S2+Li	23.5 [0.98, 68.3]	0.0004	-72.9 [-122, -2.40]	0.003
	F+S2+R	25.4 [2.86, 69.9]	< 0.001	-73.1 [-123, -3.17]	< 0.001
	S2+L	24.2 [1.54, 69.0]	< 0.001	-74.9 [-125, -4.99]	< 0.001
	F+S2+L	25.1 [2.49, 69.7]	< 0.001	-73.4 [-123, -3.19]	0.002

soil pH, it can reduce the soluble phosphorus by forming insoluble Ca-phosphates (White & Taylor 1977; Stevenson & Cole 1999). This, in turn, can negatively affect seedling survival. Liming had no significant effects on seedling survival. However, survival could be relatively low in limed plots, especially in the Netherlands. Therefore, liming should be used with caution. Although rotavation seems a good option to create suitable germination conditions, this management action should be done with caution as well since the roots of adult, extant common juniper shrubs can be damaged (Verheyen et al. 2005).

We did not detect strong effects of fencing alone. While grazing sheep, cattle, deer or rabbits can limit competition of juniper with other plant species, these animals can also lower seedling survival and successful recruitment of common juniper (Ward 1973; Clifton et al. 1997). For example, collapses of rabbit populations by myxomatosis marked periods of expansion of many common juniper populations in the UK (Ward 1973). Thus, other studies show that fencing can indeed support the survival of juniper seedlings (Broome et al. 2017).

Our results reveal a complex relationship between recruitment success, soil conditions and management, at least in the habitat we focused on (heathlands on sandy soils) since the species can occur on a wide variety of other habitats and soil types in other parts of Europe. The most important prerequisite seems to be that seeds are in contact with the mineral soil to allow germination. A second important factor is probably water availability. Soils with low percentages of organic matter and/or silt + lutum are less suitable for germination. Actions that lower those percentages, such as (very) deep sod cutting, should be avoided at drought-stressed locations. When both restrictions are met, the soil pH of the top soil is an important characteristic to determine whether liming is needed or not, although this measure should be taken with caution on nutrient-poor soils.

In sum, our study highlights the precarious condition of common juniper in the northwestern European lowlands. In this region, the species suffers from an extremely low seed viability, which can be explained by the negative influence of increasing temperatures and nitrogen deposition (Verheyen et al. 2009; Gruwez et al. 2014). These negative effects on seed viability are enhanced by the eutrophying and acidifying effects of atmospheric deposition on heathlands (Krupa 2003), which result in deteriorating conditions for germination. However, despite low seed viability, seedlings of local origins were found near our experiments. It is therefore still useful to create optimal germination conditions in places where higher seed input can be expected: near the mother shrub (although conditions there are less favourable due to direct competition) and under or near possible roosting places for birds that tend to disperse juniper seeds (mainly *Turdus* spp.; Bergman 1963; Livingston 1972; Breek 1978; García 2001) such as large stones, solitary trees or forest edges (Livingston 1972; García 2001; Hommel et al. 2009). Additional fencing will probably improve survival chances for the seedlings. Nevertheless, a significant higher input of viable seeds is necessary to lead to sustainable populations: based on a reproductive output of 176 seedlings out of 260,491 seeds in our experiment, one average mother tree would barely produce one seedling per year.

SUPPLEMENTARY FILE

One supplementary file is associated with this paper:
Principal components analysis (PCA) of the soil variables and the percentage of germinated seeds at the plot level.
https://doi.org/10.5091/plecevo.2020.1656.2153

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