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Considering both sexual and clonal reproduction could help loosen the conflict of use over *Robinia pseudoacacia*

Abstract: Black locust (*Robinia pseudocacacia*) is a widely planted tree for wood production; however, it is a very problematic invasive species through Europe. At local scale, this tree is able to invades adjacent eco-systems owing to its strong ability of asexual reproduction through root suckers. Due to this phenomenon, the role of sexual reproduction has been quite neglected at local scale. Here, we propose a double approach (i) to evaluate the ability of the species to develop under forest cover using French national forest inventory data (ii) to quantify the role of sexual and asexual reproduction at local scale using a simple visual assessment method. We evidenced that juvenile black locust regenerates in broadleaved forests where *R. pseudoacacia* did not contribute to the adult canopy; moreover, a significant higher presence in riparian forests relatively to non-riparian ones was demonstrated using national forest inventory data. Regeneration from sexual reproduction mode significantly contributes to local scale invasion (38% of the up-rooted juvenile plants) with a significantly higher ratio of sexual reproduction within oak dominated forests compared to pine dominated ones. We conclude that black locust forestry should consider that both reproduction modes contribute to the species natural regeneration and that both modes can occur under both coniferous and broadleaved forest cover. Thus, we propose to set up safety buffers around sensitive ecosystems such as natural reserves or riparian areas, to maintain black locust cultivation while minimising undesired invasions in natural areas.

Keywords: black locust, clonal and sexual regeneration, biological invasions, management guidelines

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Introduction

Black locust (*Robinia pseudoacacia* L.) is one of the exotic trees the most planted for wood production in Europe (Sitzia et al., 2016b) as it is a fast growing species and the only temperate climate tree whose wood is naturally resistant to moisture (Cierjacks et al., 2013). On the other hand, black locust is considered to be an invasive species, as it is an exotic species that can establish viable populations

and spread away from the introduction sites (Blackburn et al., 2011). It is now considered to be one of the most invasive tree species in the world (Basnou, 2009; Vilà et al., 2009). It can moreover produce severe impacts on the abiotic and biotic components of natural ecosystems due to its dynamics or its ability to fix air nitrogen (see for instance Benesperi et al., 2012; Sitzia et al., 2012). Thus, in Europe and particularly in France, the use of black locust in forestry induced a conflict of use (Dickie et al., 2014; Vítková et al., 2017) among forest managers and protected area managers. Currently, the French government and some territorial administrations recommend its planting, even by setting up financial subsidies (e.g.Conseil départemental de la Dordogne, 2021; Ministère de l'Agriculture et de la Souveraineté Alimentaire, 2023). As a consequence, the surface area of the species shows an accelerating increase in the French forests, from 100000 ha in 1979 to 131000 ha (+31%) and 220000 ha (+68%), in 2004 and 2021, respectively (Keresztesi 1980; Demené & Merzeau 2007; IGN 2021). Forest managers tend to minimize the existence and importance of the invasion process by black locust by stating it only occurs in certain habitats or ecosystems (e.g. CRPF Rhône Alpes, 2014; Préfecture de la Haute Loire, 2019). At the extreme, since the species is absent of the List of Invasive Alien Species of Union concern, they develop active lobbying towards collectivities to promote its restriction-free use in forestry since it is not legally forbidden in the EU (CRPF Nouvelle Aquitaine, 2019) or advancing improbable qualities such as creating forest fire barriers (CRPF Bretagne Pays de Loire, 2020). Still, black locust is widely spread throughout Europe, and can be found within a large diversity of habitats, in the vicinity but also at long distance, away from black locust stands and plantations (Cierjacks et al., 2013; Vítková et al., 2017) thus testifying of its invasiveness (see ecological definition in Blackburn et al., 2011). And although any organizations and administrations even in France, consider it invasive (e.g. Wegnez, 2018; Préfet de la Région Bourgogne-Franche Comté, 2019; Duval et al., 2020), there is no agreement on where and how the cultivation can be achieved to minimize invasion, necessitating adjudication at each individual conflict. Riparian forests can be defined as the forested vegetation developing along rivers, on the banks, the floodplains or terraces, under direct potential interactions with the stream (Naiman et al. 1998). In South-West France, local managers indicated that the species is particularly developing in riparian forests (GT IBMA 2016). The analysis of the regeneration of black locust under forest cover and in particular in riparian forests, and information on some reproduction life history traits could help decision-making in forestry to minimize its invasiveness.

Several traits may promote species invasiveness such as, for instance, an enhanced competitive ability (Gioria & Osborne, 2014), but propagule pressure would also contribute. Asexual reproduction could facilitate the early settlement of the species, in particular long lived organisms such as trees (Baker, 1967; Barrett, 2015). Supporting this statement, modifications of the mating system were observed for several species (Hollingsworth & Bailey, 2000; Rambuda & Johnson, 2004; Petanidou et al., 2012), as for example, the water hyacinth: indeed, *Eichornia crassipes* shifted from a sexual reproductive system in its native range towards a fully clonal reproductive system in its invasive range (Barrett et al., 2008). However, black locust is able to reproduce both sexually and asexually. Thus, both reproductive systems contribute to the species' spreading success. Based on molecular markers analyses, it was shown that black locust seemed to express more clonal reproduction within its European invasive range compared to its native range (Bouteiller et al., 2019). At fine scale, it has been demonstrated that asexual reproduction through root suckers allows black locust to rapidly colonize new sites in close proximity to the planting sites (e.g. Krízsik & Körmöczi, 2000; Jung et al., 2009; Kurokochi et al., 2010). Moreover; wind- or water-mediated seed dispersion permits long-distance spread to reach new sites away from initial population sources (von der Lippe & Kowarik, 2007; Säumel & Kowarik, 2013). Furthermore, European populations present a higher germination rate than the native American populations (88% *versus* 60%, Bouteiller at al., 2021) which could facilitate the settlement of distant populations, close to roads, railways and rivers which serve as dispersal axis. In Japan, indirect evaluations using SSR molecular markers showed that both seeds and root suckers have contributed to the short distance spreading of black locust in riparian forests (Kurokochi et al., 2010; Kurokochi & Hogetsu, 2014). Nonetheless, direct quantification of the relative contribution of sexual and asexual reproduction to the established regeneration of black locust in forested areas has yet to be evaluated.

Here we first aimed at evaluating the patterns of regeneration of black locust under forest cover at a country scale using the French forest inventory to answer the following questions: can black locust regenerate under different forest covers? Is the species distribution positively skewed towards riparian forests which often harbor sensitive protected habitats? We then investigated the role of sexual and asexual reproduction in black locust regeneration at a local scale in managed forests of Southwest France: are sexual (from seeds) and asexual (from root suckers) reproduction modes contributing equally to black locust regeneration under forest cover?

Methods

Black locust regeneration in France using the national forest inventory

To investigate the repartition of black locust regeneration in the different forest types, we used the 3rd French national inventory (65710 plots, 3rd inventory 2005–2014, IGN National Geographic Institute, https://inventaire-forestier.ign.fr/dataIFN/). We extracted from the database all the plots with presence of *Robinia pseudoacacia* (Fig. 1A). During field measurements by IGN, data were separated according to the diameter of the individuals: adult trees defined as individuals with a minimum diameter at breast height of 7.5 cm (IGN, online) are in the tree table, and juveniles (seedlings or resprouts) defined

as individuals below this diameter are in the understory flora table. We thus calculated the proportion of plots with adults only, adults plus juveniles, or juveniles only. Data were further imported in Qgis (GIS 3.10.10-A Coruña, https://www.qgis.org/) using the North Pole Azimuthal Equidistant projection, in order to be able to perform distance calculations correctly in all directions and calculate a river buffer. To evaluate the potentially higher vulnerability of riparian forests to black locust invasion, we used the river network layer provided in Andreadis et al. (2013; http://gaia.geosci.unc.edu/rivers/). Geomorphological and ecological characteristics of riparian forests are varying according to the climate, vegetation type and river hydrology, producing several types of habitats (Louvel et al., 2013), with width varying from a few dozens to several hundred meters (see
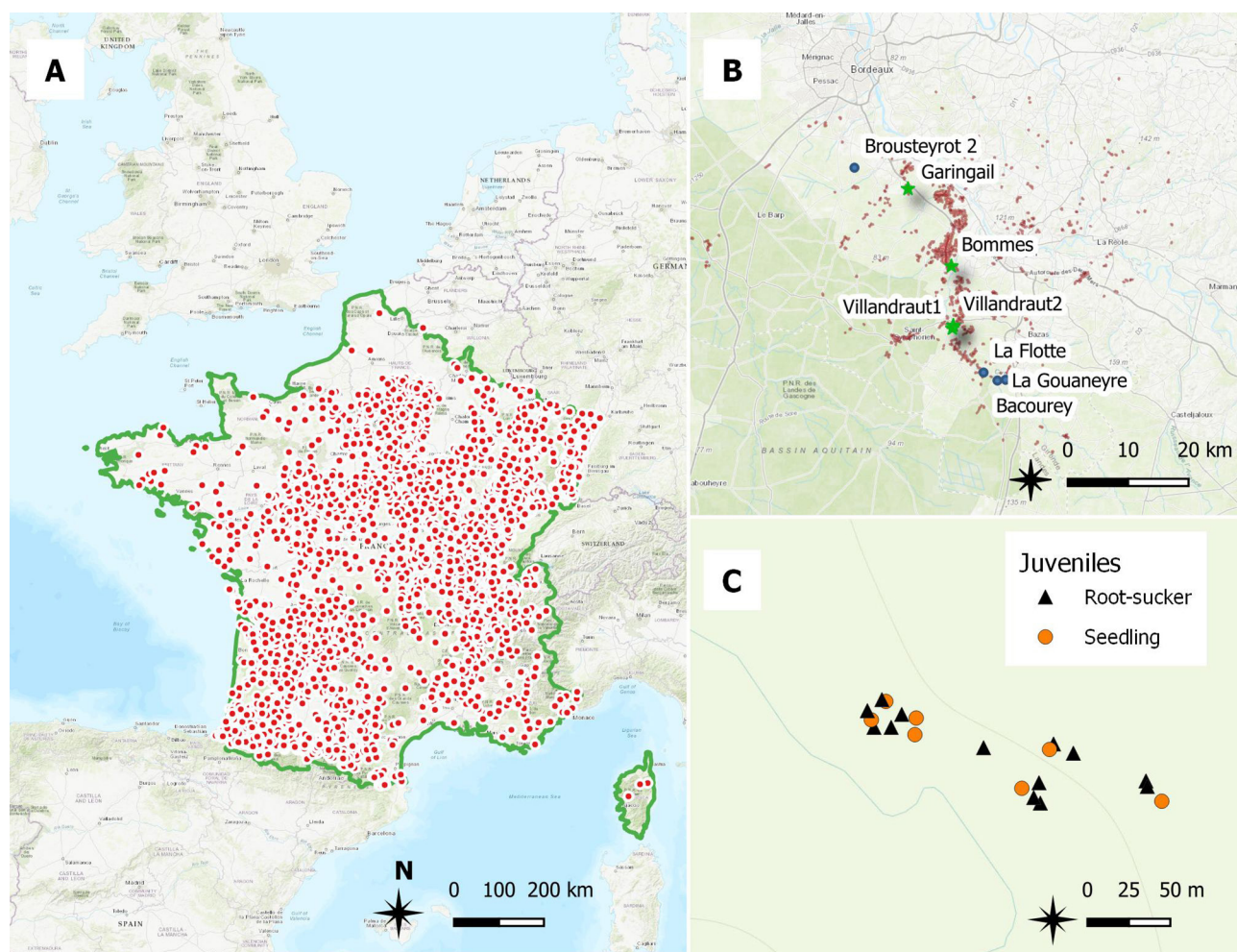

Fig. 1. (A) French national forest inventory plots with presence of black locust (n = 3831, red dots), as extracted from the 3rd NFI to evaluate the global pattern of regeneration of the species under forest cover. (B) Location of the sampled sites in the Ciron valley in South-western France, used to evaluate the role of sexual reproduction in regeneration dynamics of black locust under forest cover: oak stands – green stars and pine plantations – blue dots. The red areas on the map corresponds to the monospecific stands of black locust, extracted from the IGN French forest cover database (BD Foret v2) (C) Example at the La Gouaneyre site of the spatial repartition of the juveniles: root suckers – black triangles and seedlings – orange dots. Background map is ESRI World Topo(https://qms.nextgis.com/geoservices/519/) and was used under Qgis 3.10.10-A Coruña

for instance Keller et al., 1993; Metzger et al., 1997; Naiman et al, 1998). As such, in a generic approach, we used a common buffer of 100 meters around the layer of rivers (vector; geoprocessing tools; buffer). to extract plots in the buffer, as a proxi of riparian forests.

To test if the presence of black locust was higher in riparian forests than the random probability due to forest inventory samplings over the whole French territory, we analyzed the count data of plots with and without black locust in or out of the rivers' buffers using a χ^2 independence test.

Quantification of established sexual vs asexual regeneration

During spring 2017, 8 sites were selected in the South West of France in the protected natural area of the Ciron valley (Fig. 1B; Supplementary Table S1) where black locust is otherwise largely cultivated and managed in monospecific plantations (Fig 1B, black locust areas in Gironde, 2017, Base de Données Forêt, BD FORET v2, IGN, https://geoservices.ign.fr/ressource/191361). Thus, as we intended to evaluate the potential role of sexual or asexual reproduction in regeneration at local scale, sites were

Fig. 2. Young individual of black locust with the root system extracted from the ground. On the left, the individual is a seedling exhibiting a branched root system. On the right, the individual is a root sucker, where a large horizontal root can be observed from which emerge the stem and the secondary roots. Photographs by XP Bouteiller

selected so that they were not such black locust plantations but we made sure that at least one mature adult black locust tree was located within 10 m from the studied plot. Then, the dominant native species of the plot was either maritime pine (*Pinus pinaster*) or pedunculate oak (*Quercus robur*, with or without *Quercus pyrenaica)*, corresponding to two forest types: artificial pine plantations and oak woodlands. We selected plots with no apparent recent management practices such as tree cutting, soil ploughing, understory removal.

In each site, 13 to 27 small individuals of black locust (between 1–2 cm of diameter at 1.3 m of height), distant from one another by 5 m at least (Fig 1C) were randomly selected in order to determinate if they originated from a seedling (sexual reproduction) or a root sucker (asexual reproduction). Dimensions were selected in order to avoid both too old and too young individuals. For each individual, the root system was manually extracted from the ground and visual inspection of the root system allowed to determine if the individual was a root sucker or a seedling (Fig. 2). Indeed, seedlings and root suckers demonstrated strong differences in their root system architectural development: seedlings exhibited a branched system with fine and medium roots, while root suckers presented a large horizontal root from which departed the upward stem and the medium roots.

On each site, proportion of seedlings and root suckers was calculated. A χ^2 test of independence was performed to test if a link existed between the proportion of seedlings and the dominant native species.

Furthermore, a generalized linear model using a logit link was performed since the response variable is a binary variable, seedlings vs non seedlings (reported as 1 or 0 respectively). Three models were compared based on AIC: 1) null model (no dependent variable, only a mean effect), 2) dominant species as an explanatory variable and 3) dominant species and population as explanatory variables. Analyses were achieved using R v3.3.1 (R Development Core Team, 2016).

Results

Occurrence of regeneration of black locust in the French forests

In total, in the 3rd French national inventory, there were 3831 plots with black locust (5.8% of the inventoried plots): 8 with adult trees only, 1835 with juveniles only and 1988 with both juveniles and adults. Thus, almost 50% of the juveniles were found in plots without adults of black locust. The dominant species on the 3823 (i.e. 1835+1988)
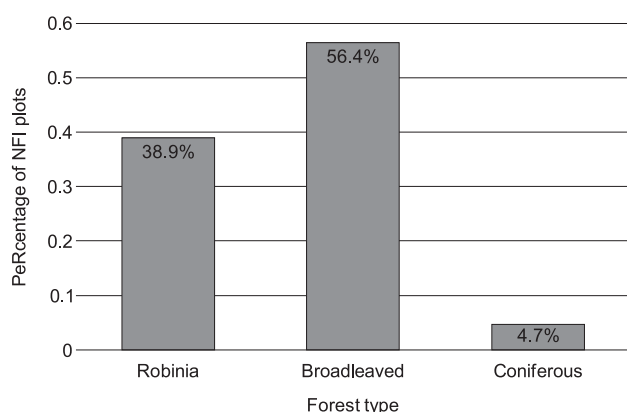
Fig. 3. Repartition of the 3rd French NFI plots containing black locust according to the forest type, as defined by the composition of the canopy: *Robinia pseudoacacia*, other broadleaved species or coniferous species

Table 1. Chi-square test results based on the number of plots in or out of the river buffer, for plots with *Robinia pseudoacacia* or without (other)

Species	Plots in the river buffer	Plots out of the buffer	% in buffer	Chi-square	p
R. pseudoacacia	180	3651	4.70	36.041	1.932 E-9
Other	1833	60046	2.96		

plots presenting juveniles was black locust for only 38.9% of the plots (Fig. 3), 4.7% a coniferous species (mostly *Pinus pinaster*, *Pinus sylvestris*) and 56.4% a broadleaved species (mostly *Quercus robur*, *Fraxinus excelsior*, *Quercus petraea*, *Castanea sativa*, *Quercus pubescens*, *Carpinus betulus*, *Acer pseudoplatanus*; see full list in Supplementary Table S2).

The analysis of the plots containing black locust was achieved to test if the presence of black locust in riparian forests was higher than expected from a random sampling of French forest or not. As can be seen in Table 1, the χ^2 test was significantly different from zero, indicating the existence of a positive relationship between black locust occurrence and the riparian forests. This correlation is valid whether we considered plots with black locust juveniles only or plots with adults and juveniles together (no difference in the test, $\chi^2 = 0.859$, $p = 0.354$).

Both sexual and asexual reproduction contributes to local regeneration

We reported the occurrence of sexual reproduction of black locust under forest canopy by the study of its established regeneration, at a local scale in South West France forests. Still, asexual reproduction remained dominant. Indeed, in the sampled plots, black locust seedlings represented on average 37.9% (IC95% [30.4–45.5]) of the juveniles, opposed to root suckers. However, a large variation in
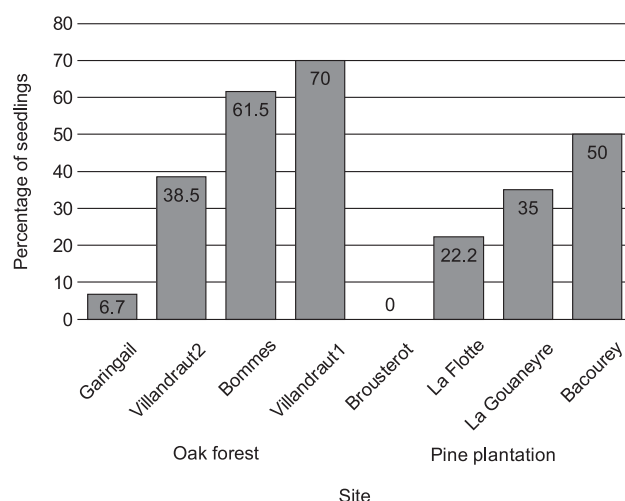

Fig. 4. Percentage of black locust seedlings in each sampled site from the Ciron valley in South-western France (calculated as the ratio between the number of seedlings and the total number of juveniles). Bar color is related to the native dominant species with green: oak forest, and blue: pine plantation. Absolute numbers of seedlings and root-suckers per site are provided in Table S1

seedlings proportion was observed between sites, with values ranging from 0% to 70% (Brousteyrot and Villandraut 1, respectively, Fig. 4). There is a significant association ($\chi^2 = 5.91$, $p = 0.015$) between the proportion of black locust seedlings and the forest type: a lower proportion of seedlings was observed in the pine plantations (28.6%) whereas it was equal to 51.3% in the oak woodlands. The AIC generalized linear model was lower for the model with forest type as explanatory variable (model 2) than for the null model (207.0 vs 211.8).

Discussion

This study demonstrated that both sexual and asexual reproduction contributed to black locust established regeneration at local scale: indeed, in all sites except one, black locust seedlings were found. Similarly, the analysis of the genetic diversity of black locust populations at the landscape scale in Japan (Kurokochi & Hogetsu, 2014) or at the global scale in its European and native ranges (Bouteiller et al., 2019) did show that the diversity level implied the existence of sexual reproduction and spread. Still, most studies concluded that sexual reproduction was only successful in open areas, as germination did not result in established regeneration under forest cover (Cierjacks et al., 2013; Vítková et al., 2017). Our approach adds significant insights by evidencing the role of sexual reproduction in the success of regeneration under both pine or oak forest cover. This established regeneration is either related to black locust seeds that can persist several years in the soil seed

bank (Cierjacks et al., 2013), or from recent dispersal events from mature trees.

Moreover, the regeneration mode (sexual origin or not) was influenced by the forest type, with a larger proportion of root suckers within the pine dominated forests. Our main hypothesis is that root sucker production was favored here because of anthropogenic disturbances: indeed, the intense management practices in maritime pine plantations make use of many mechanical interventions such as brush cutting with shallow plowing (at planting, three years after planting, then every five years on average, CRPF Aquitaine 2015). Such mechanical disturbances promote black locust asexual regeneration by damaging the existing horizontal roots of black locusts (Cierjacks et al., 2013; Vítková et al., 2017).

The analysis of the French NFI data clearly demonstrated that regeneration of black locust largely occurred under broadleaved or coniferous species forest canopy, including plots without the presence of adults of black locust. This evidences its ability to invade forests under several kinds of canopies. For central and southern Europe, two recent reviews stated that black locust invades mixed stands of fast growing species with light canopy cover (Vítková et al., 2017, 2020) ; but they also indicated that black locust seemed able to develop under more closed canopy and to over-compete oak species. However, our results suggest that black locust can actually develop under fast growing species with light canopies but also under slow growing species with denser canopies Indeed, data from the French National Forest Inventory data from Gironde and Landes departments indicated that the average basal area of Oak dominated stands (n = 560 plots) was 32% higher than that of Pine plantations (n = 1369 plots). Since leaf biomass or area index is proportional to tree or stand basal area (see for instance Neumann et al. 2016), this would correspond to higher leaf area index in oak woodland, as indeed observed by Bréda (2002; at least +25% LAI in *Quercus* versus *Pinus* stands).

Moreover, Vítková et al. (2017) also pointed out that the species developed better away from rivers (except on high slope banks), due to limitation by waterlogging. However, the analyses of the location of invaded plots in France clearly demonstrated the ability of black locust to frequently develop in riparian forests, as defined by the 100 m wide buffer alongside rivers. Since we reported that black locust juveniles in the river buffers would occur with or without adults, this underlined the higher sensitivity of riparian forests to black locust invasion. It could be a consequence of the role of rivers in black locust dynamics: rivers are effective dispersers away from planting sites as was demonstrated in Germany using floating pods (Säumel & Kowarik, 2013), providing seeds that created new patches of black locust in

riparian forests of the Akgagawa River Basin in Japan (Takahashi et al., 2008 in Morimoto et al., 2010). The apparent differences in the sensitivity of riparian areas to black locust settlement between what was observed Central Europe (Vítková et al. 2017) could have two sources: first, we defined riparian forests using a common geographic buffer which covers several kinds of topography and water regimes of the river basins where the riparian forests were growing while Vítková et al. (2017) examined floodplains in particular, submitted to flood regimes. Second, there are variations in the climatic zones between our study and Central Europe, and we have results similar to that of colleagues in Italy who observed the same occurrence of regeneration in riparian areas (Ubaldi, 2013 in Sitzia et al., 2016b).

Conclusions

A management guideline was proposed in Italy to control black locust propagation out of forestry plots by focusing on its clonal propagation abilities: (i) avoid coppicing practices to reduce root suckers (ii) use buried barriers to avoid underground spreading (Sitzia et al., 2016a). However, we stress out that the role of sexual reproduction in the local extension of black locust must be taken into account in any case of black locust cultivation to minimize its invasion, and avoiding coppicing only will not avoid fruit production and spread.

It was clear from previous studies, that black locust invasion produces dense thickets in open areas (Sitzia et al., 2016b; Vítková et al., 2017, 2020), and we demonstrated that it can effectively regenerate by both root suckers and seedlings under forest canopy such as pine or oak. This would imply that maintaining permanent forested areas around black locust plantations would not be sufficient to avoid species spread outside the plantation. A previous guideline based on a typology of black locust plantations mostly proposed forest management practices within the stands to limit spreading (Sádlo et al. 2017); interestingly, they pointed out the use of adjacent cultivated ploughed areas as buffers to limit the spread of black locust from both seedlings or root-sucker. Still this proposal seems contradictory to our findings where harrowing appeared to enhanced black locust spreading by root suckers.

Finally, the frequent occurrence of black locust in riparian forests suggests a high sensitivity of these areas to black locust invasion. Therefore, considering the quasi-impossibility to set up management practices to avoid black locust spread outside plantations, we suggest that the best suitable practice in order to develop a cultivation of black locust in France while reducing conflicts around its use would consist in

setting these plantations away from vulnerable habitats or protected areas. Setting up safe zones around the sensitive habitats could be more efficient than buffers around plantations or management practices within the plantations. The exact distance of black locust spread is probably depending on local conditions, such as dominant winds or topography; it was estimated at 500 meters in Germany (Landeck & Hildmann, 2022). So safe zones of several hundred meters could be considered to protect sensitive habitats from regeneration coming out of any black locust plantations.

Acknowledgements

Data availability

The Ciron valley dataset used in this publication will be made available on open science framework after acceptance. French NFI data are already available on IGN website (https://inventaire-forestier.ign.fr/dataIFN/).

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