RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

UN DECADE ON ECOSYSTEM RESTORATION

RE-NEW (OPINION) ARTICLE

Seeding or planting to revegetate the world's degraded land: systematic review and experimentation to address methodological issues

Alexandro B. Leverkus[1,2,3], Alba Lázaro González[1], Enrique Andivia[4], Jorge Castro[1], María Noelia Jiménez[5], Francisco B. Navarro[6]

Revegetation is key to achieve the goals of the UN Decade on Ecosystem Restoration. For many situations and plant species, selecting direct seeding or planting can define revegetation success. However, there is no clarity about when one method should be preferred over the other, partly driven by methodological difficulties that preclude avoiding bias during experimentation. To move the debate forward, (1) we propose a systematic review of the studies that compare seeding and planting, including how they have handled bias; and (2) we describe an ongoing experiment that tests different ways to handle bias when comparing seeding with planting.

Key words: afforestation, assisted regeneration, nursery cultivation, reforestation, sowing, systematic review protocol

Conceptual Implications

- Electing to revegetate through seeding or planting can modulate the biotic and abiotic stresses suffered by seedlings and affect restoration success.
- Evaluating the balance between these two key revegetation alternatives involves choosing between unavoidable sources of bias.
- Bias may result from differences in the demographic stage of seedlings resulting from seeding and planting, seed origin and storage, seed quality, and revegetation year.
- We outline the objectives and protocol for a new systematic review and describe an ongoing experiment which, combined, aim to produce novel insights on the seeding vs. planting debate and offer ways to handle bias.

The UN Decade on Ecological Restoration provides a unique opportunity to tackle the challenge of restoring the 2 billion ha of degraded land around the world (Cernansky 2018). Succeeding in such objectives could provide important benefits related to ecosystem service supply and climate change mitigation (Chazdon 2008; Nave et al. 2018). Revegetation constitutes a fundamental step in this effort. The ambitious plans for revegetation also highlight its noteworthy economic importance, as an entire industry related to seed collection and seedling production produces employment and community involvement, whereas the concomitant costs stress the need for guaranteeing high revegetation success (Kimball et al. 2015).

Ensuring the success of revegetation requires selecting appropriate species given current and projected environmental conditions (Leverkus et al. 2021) and the use of techniques that promote success. Revegetation success can be low even under historical conditions (e.g. Rey Benayas et al. 2005), which constitutes a waste of economic resources and the fading of the prospect of a restored habitat. Major drivers of revegetation failure may include both adverse biotic and abiotic conditions. For instance, long, dry summers or poor, shallow soils can limit seedling survival and

Author contributions: ABL conceived the manuscript and the proposed review following discussion with FBN, JC, MNJ, EA. FBN designed and implemented the experiment aided by JC, MNJ, ABL; ABL, ALG made the initial literature searches and refined the review protocol; ABL wrote the first draft; all authors provided input and approved the manuscript.

[1]Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, Granada, 18071, Spain
[2]Laboratorio de Ecología, Instituto Interuniversitario de Investigación del Sistema Tierra en Andalucía (IISTA), Universidad de Granada, Granada, 18006, Spain
[3]Address correspondence to A. B. Leverkus, email leverkus@ugr.es
[4]Departamento de Biodiversidad, Ecología y Evolución, Universidad Complutense de Madrid, Spain
[5]Departamento de Botánica, Facultad de Farmacia, Campus de Cartuja s/n, Granada 18071, Spain
[6]Área de Agricultura y Medio Ambiente, Instituto Andaluz de Investigación y Formación Agraria, Pesquera, Alimentaria y de la Producción Ecológica (IFAPA), Junta de Andalucía. Centro Camino de Purchil, Camino de Purchil s/n, Granada 18004, Spain

doi: 10.1111/rec.13372
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13372/suppinfo

performance (Rey Benayas et al. 2015; Leverkus et al. 2015*a*). Biotic stress, primarily through herbivory, seed predation, and competition, can also cause great losses (Löf & Welander 2004; Rey Benayas et al. 2015; Castro & Leverkus 2019; Löf et al. 2019). Both kinds of stresses can be influenced by the method employed for revegetation, so it is essential to identify the causes of failure and propose techniques to address them.

The Seeding or Planting Dilemma

Current methods for revegetation with many trees and shrubs rely mostly on the outplanting of nursery-grown seedlings. The alternative for many species, direct seeding of seeds in the field, is often discarded due to the risk of low germination and establishment rates, partly driven by high seed predation and the vulnerability of young seedlings (Allen et al. 2001; Palma & Laurance 2015; Leverkus et al. 2015*b*). Seedling planting has several advantages over seeding, such as generally faster seedling growth and establishment, and the avoidance of seed predation (Allen et al. 2001; Löf et al. 2004). Seeding operations, on the other hand, are easier to carry out and generally less costly (Löf et al. 2004). Seeding also reduces the risk of transferring plant diseases from nurseries to the field (Sánchez et al. 2005). Root morphology may also be affected by the choice of revegetation method, with implications for plant access to soil resources. For instance, in the case of oaks (*Quercus* spp.), the tap root of nursery-grown seedlings is often damaged or anomalously shaped when grown in containers, or pruned in the case of bare-root transplanted seedlings (Allen et al. 2001). This may lead to a shallower or unnaturally developed root system with vascular problems, less access to soil resources, and ultimately to lower seedling performance given some degree of water shortage (Pemán et al. 2006; Tsakaldimi et al. 2009). As the relevance of different stressors for revegetation gradually changes—for instance through the commercialization of new seed protectors that prevent their predation (Lof et al. 2019) and the intensification of droughts and disturbances globally (Leverkus et al. 2021)—the consequences of revegetation method on plant survival and performance need renewed evaluation.

Empirically evaluating the performance of seeding and planting represents considerable methodological challenges related to the risk of bias between the two methods. Seeding and planting are necessarily accompanied by confounding factors so that, when designing experiments, researchers must select among an array of possible trade-offs among different confounders. For instance, if seedlings and seeds are placed in the field simultaneously, thereby homogenizing weather conditions after revegetation between the two treatments, the experiment suffers from comparing planted seedlings that are 1 or more years older than those from sown seeds, as well as from the wrong seeding or planting season if both differ. Contrarily, if seeds are sown 1 year ahead of planting to control for seedling age, the effect of revegetation method cannot be differentiated from idiosyncratic weather differences between revegetation years. The comparison of methods can be further obscured by differences in cultivation techniques, the year of seed collection, the characteristics of seeds, and even the identity of the maternal plant (Dey et al. 2008; Palma & Laurance 2015; Löf et al. 2019). The comparability of experimental seeding and planting treatments may also be modulated by the responses being measured, combined with the timing of measurement. Demographic statistics of revegetated species are among the most common response variables in revegetation studies (Ceccon et al. 2016), yet these may be quite susceptible to bias due to the demographic differences inherent to both methods. This makes responses biased (such as seedling survival, which is related to seedling age) or not comparable at all (such as emergence probability, which cannot be measured on planted seedlings). Broader variables related to restoration targets, such as habitat quality indicators, could provide more suitable comparisons between methods (Fraser et al. 2015). It may be necessary to further define success in terms of output per unit input, for instance change in native plant cover obtained per unit money spent (Kimball et al. 2015). Despite the key importance of such methodological issues, we are not aware of studies that have assessed the trade-offs between different ways of addressing confounding factors and the associated risk of bias in seeding versus planting experiments, nor of reviews aiming to produce a broader picture of what has been done to date and how to move this debate forward.

Ways Ahead

To advance this topic, we are currently working on two fronts.

(1) A systematic review. Some reviews have previously addressed direct seeding (e.g. Ceccon et al. 2016; Grossnickle & Ivetić 2017; Löf et al. 2019) and the success of seeding compared to planting (Dey et al. 2008; Palma & Laurance 2015). However, to our knowledge, none of them has followed a reproducible, systematic approach, specifically targeted studies comparing the two revegetation methods. or reviewed the handling of bias in experiments. In Supplement S1 we present the protocol of our systematic review; its publication aims to increase the transparency and robustness of the review process and reduce potential for review bias (Kupferschmidt 2018). The protocol pre-defines our objectives, search strategy, article selection criteria, screening methodology, and data extraction strategy. The review is designed under the methodological standards set by the Collaboration for Environmental Evidence and the Cochrane Handbook for Systematic Reviews (Higgins & Green 2011; Koricheva et al. 2013).

(2) An experiment to compare the performance of planted holm oak (*Quercus ilex*) seedlings with seedlings emerged from sown acorns while simultaneously aiming to test the validity of different ways of comparing them. The experiment was set up in 2016–2018 in four localities across Andalusia (southern Spain), each of which includes six independently fenced blocks divided in two plots for an irrigation treatment. Each plot has 10 oak seedlings grown from local seed under each of eight methods (*treatments* in Table 1). For each seedling, we have kept track of the mass of the acorn and the identity of the maternal tree to control for these potential sources of variability (maternal trees were the same for acorns collected in 2016 and 2017 when possible).

Table 1. Characteristics of experimental revegetation treatments in an ongoing experiment with the holm oak (*Quercus ilex* subsp. *ballota*). The last two columns refer to the comparability of the seeding treatments with the planting treatments. Treatments *a* and *b* involve two seeding treatments each: one with and one without seed shelters to prevent acorn predation by rodents (Leverkus et al. 2015*b*); removed from the table for simplicity of presentation.

Treatment	*Collection Year*	*Field Year*	*Method*	*Description*	*Strength*	*Weakness*
a	2016	2017	Seeding	Acorns sown at the start of seedling cultivation	Same seed batch and seedling age as planting	Different year of revegetation than planting
b	2016	2018	Seeding	Acorns stored 1 year at 0°C prior to seeding. Seeding simultaneous to outplanting	Same seed batch and year of revegetation as planting	Loss of seed viability during storage; different seedling age than planting
c	2017	2018	Seeding	Acorns collected 1 year later and sown at the time of outplanting	Same year of revegetation as planting; no storage-induced seed viability loss	Different seed batch than planting, albeit from same mother trees; different seedling age
d	2016	2018	Planting	Common plastic containers with self-root-pruning system and anti-spiraling system in the inner cell walls (300 cm^3)		
e	2016	2018	Planting	Deep, biodegradable containers (50 cm deep, 600 cm^3)		
f	2016	2018	Planting	Deep plastic containers with open bottom (50 cm deep, 600 cm^3)		

We are closely monitoring plant performance and aim to assess the differences in outcomes of the seeding/planting dilemma resulting from differences in the way in which the potential sources of variability are controlled.

The selected combination of treatments in our experiment allows answering an array of questions to assess the performance of plants obtained through seeding and planting. For example, does planting nursery-grown seedlings produce more competitive seedlings than seeding acorns of the same maternal tree and seed size and collection year (treatments *a* vs. *d* in Table 1)? Does this effect vary with increasing drought (differences in the comparison of treatments *a* versus *d* across irrigation treatments and localities)? Moreover, the experiment is designed to assess the differences in the balance of seeding vs. planting when different planting techniques are employed, when seed predation by rodents is controlled for or not, and when different approaches are employed to control bias. For instance, does comparing seeding vs. planting produce different outcomes if seedlings are grown in normal containers (*a* vs. *d*) than if containers allow developing a longer root (*a* vs. *e–f*)? And, how does seeding compare to planting if seedlings are similarly aged (treatments *a* vs. *d*) vs. if revegetation is conducted simultaneously yet at the cost of comparing planted seedlings with younger sown seedlings plus sown acorns coming from a subsequent cohort of acorns (*c* vs. *d*) or from the same cohort but after 1 year of storage (*b* vs. *d*)?

Conclusion

The sensitivity of revegetation efforts to environmental stressors may greatly depend on the selection of the planting or seeding method, yet we still lack capacity to understand the results of experiments in the light of the limitations imposed by unavoidable sources of bias. The combined purpose of our proposed review and ongoing experiment is to produce solid insights into the drivers of the balance between both revegetation methods as well as setting guidelines for the future assessment of seeding vs. planting success. This may ultimately help improve our capacity to address the colossal goals of the UN Decade on Ecosystem Restoration.

Acknowledgments

This work is funded by grants RTI2018-096187-J-100 from FEDER/Ministerio de Ciencia, Innovación y Universidades, AVA201601.19 (NUTERA-DE), AVA2019.004 (NUTERA-DE II) co-financed (80%) by the FEDER Program, and P18-RT-1927 from Consejería de Economía, Conocimiento, y Universidad de la Junta de Andalucía, also co-financed by the FEDER program.

LITERATURE CITED

Allen JA, Keeland BD, Stanturf JA, Clewell AF, Kennedy Jr. HE (2001) A guide to bottomland hardwood restoration. USDA Forest Service General Technical Report SRS–40 132

Castro J, Leverkus AB (2019) Effect of herbaceous layer interference on the post-fire regeneration of a serotinous pine (*Pinus pinaster* Aiton) across two seedling ages. Forests 10:74

Ceccon E, González EJ, Martorell C (2016) Is direct seeding a biologically viable strategy for restoring forest ecosystems? Evidences from a meta-analysis. Land Degradation and Development 27:511–520

Cernansky R (2018) How to rebuild a forest. Nature 560:542–544

Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458–1460

Dey DC, Jacobs D, McNabb K, Miller G, Baldwin V, Foster G (2008) Artificial regeneration of major oak (*Quercus*) species in the eastern United States—a review of the literature. Forest Science 54:77–106

Fraser LH, Harrower WL, Garris HW, Davidson S, Hebert PDN, Howie R, et al. (2015) A call for applying trophic structure in ecological restoration. Restoration Ecology 23:503–507

Grossnickle SC, Ivetić V (2017) Direct seeding in reforestation – a field performance review. Reforesta 4:94–142

Higgins J, Green S (eds) (2011) Cochrane handbook for systematic reviews of interventions version 5.1.0. John Wiley & Sons, Chichester, United Kingdom

Kimball S, Lulow M, Sorenson Q, Balazs K, Fang Y, Davis SJ, Connell MO, Huxman TE (2015) Cost-effective ecological restoration. Restoration Ecology 23:1–11

Koricheva J, Gurevitch J, Mengersen K (eds) (2013) Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton, New Jersey and Oxford, United Kingdom

Kupferschmidt K (2018) A recipe for rigor. Science 361:1192–1193

Leverkus AB, Castro J, Delgado-Capel MJ, Molinas-González C, Pulgar M, Marañón-Jiménez S, Delgado-Huertas A, Querejeta JI (2015a) Restoring for the present or restoring for the future: enhanced performance of two sympatric oaks (*Quercus ilex and Quercus pyrenaica*) above the current forest limit. Restoration Ecology 23:936–946

Leverkus AB, Rojo M, Castro J (2015b) Habitat complexity and individual acorn protectors enhance the post-fire restoration of oak forests via seed sowing. Ecological Engineering 83:276–280

Leverkus AB, Thorn S, Gustafsson L, Noss R, Müller J, Pausas JG, Lindenmayer DB (2021) Environmental policies to cope with novel disturbance regimes–steps to address a world scientists' warning to humanity. Environmental Research Letters, 16:021003. http://dx.doi.org/10.1088/1748-9326/abdc5a

Löf M, Welander NT (2004) Influence of herbaceous competitors on early growth in direct seeded *Fagus sylvatica* L. and *Quercus robur* L. Annals of Forest Science 61:781–788

Löf M, Thomsen A, Madsen P (2004) Sowing and transplanting of broadleaves (*Fagus sylvatica* L., *Quercus robur* L., *Prunus avium* L. and *Crataegus monogyna* Jacq.) for afforestation of farmland. Forest Ecology and Management 188:113–123

Löf M, Castro J, Engman M, Leverkus AB, Madsen P, Reque JA, Villalobos A, Gardiner ES (2019) Tamm review: direct seeding to restore oak (*Quercus* spp.) forests and woodlands. Forest Ecology and Management 448:474–489

Nave LE, Domke GM, Hofmeister KL, Mishra U, Perry CH, Walters BF, Swanston CW (2018) Reforestation can sequester two petagrams of carbon in US topsoils in a century. Proceedings of the National Academy of Sciences 115:201719685

Palma AC, Laurance SGWW (2015) A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? Applied Vegetation Science 18:561–568

Pemán J, Voltas J, Gil-Pelegrin E (2006) Morphological and functional variability in the root system of *Quercus ilex* L. subject to confinement: consequences for afforestation. Annals of Forest Science 63:425–430

Rey Benayas JM, Navarro J, Espigares T, Nicolau JM, M a Zavala (2005) Effects of artificial shading and weed mowing in reforestation of Mediterranean abandoned cropland with contrasting *Quercus* species. Forest Ecology and Management 212:302–314

Rey Benayas JM, Martínez-Baroja L, Pérez-Camacho L, Villar-Salvador P, Holl KD (2015) Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland. New Forests 46:841–853

Sánchez ME, Andicoberry S, Trapero A (2005) Pathogenicity of three *Phytophthora* spp. causing late seedling rot of *Quercus ilex ssp. ballota*. Forest Pathology 35:115–125

Tsakaldimi M, Tsitsoni T, Ganatsas P, Zagas T (2009) A comparison of root architecture and shoot morphology between naturally regenerated and container-grown seedlings of *Quercus ilex*. Plant and Soil 324:103–113

Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Systematic review protocol.

Coordinating Editor: Stephen Murphy

Received: 20 January, 2021; First decision: 9 February, 2021; Revised: 11 February, 2021; Accepted: 16 February, 2021