Direct Seeding in Reforestation-A Field Performance Review

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Abstract

Direct seeding has been considered a forest restoration option for centuries. Over the past half century, the use of this practice has declined in developed countries as forest regeneration programs have advanced with the production of quality seedlings that can successfully establish restoration sites. Direct seeding is being reconsidered as a restoration option as the potential size of the worldwide forest restoration program has grown because of massive deforestation in third-world nations and due to global climate change. This review examines direct seeding from a number of perspectives. First, merits of using this practice in restoration programs are defined. Major merits of this option are that it can be done quickly, over hard to reach and large disturbed areas, and at a relatively low cost. Second, current research findings from restoration programs are discussed. The major finding is that seedling establishment rates are low (i.e. typically around 20% of seeds planted) due to site conditions, seed predation and vegetation competition, and field performance (i.e. survival and growth) is lower than planted seedlings. Third, operational practices for the application in restoration programs are reviewed. To successfully conduct direct seeding programs practitioners need to consider seedbed receptivity, seed distribution and seeding rate. Fourth, potential new practices are presented. Some of these new practices attempt to create a more effective means to disperse seed across the site, minimize seed predation or create a more favorable microsite environment. This review provides a synthesis of what is known about direct seeding, thereby allowing practitioners to make a rational decision of whether to apply this practice towards their forest restoration program.

Keywords

Direct Seeding; Reforestation; Forest Restoration; Seedling Establishment

Contents

1 Introduction

The use of direct seeding with tree species has been an ongoing silvicultural practice in forest restoration programs for centuries. The first references discussing the application of direct seeding, as a reforestation practice, goes back to the 14th century (cited by Willoughby et al. 2004). Direct seeding became a viable option during sustainable forestry programs in the 19th century (reviewed by du Cros et al. 2004; Chick 2004; Ammer and Mosandl 2007). In fact, many methods discussed by Toumey (1916) (i.e. broadcast or drilled seeding in strip, line, hole or spot distribution patterns) are still considered standard practices today. Prior to the development of large-scale nursery programs to produce seedlings, direct seeding or partial seeding (i.e. the combination of direct seeding and leave-seed trees) were considered the 'best practice' for forest regeneration programs to reestablish a forest stand (Smith 1962).

Recently, there is an increasing interest in the use of direct seeding as an alternative to seedling planting. This is because the amount of forest restoration required worldwide is overwhelming. The last Forest Resources Assessment (FAO 2015) reported a global net forest loss of 3.3 x 10^6 ha $year^{-1}$ from 2010 to 2015. This has resulted in the need to restore up to two billion hectares of forest sites worldwide (Minnemayer et al. 2011). Forest losses over the past 25 years have been highest in third-world nations (Sloan and Sayer 2015) and recently, the UN declared the need to restore forest to 350 million hectares of degraded land by 2030 to tackle climate change (United Nations 2014). Thus, low cost options are required to meet the size of this worldwide restoration program; such as direct seeding (Fischer et al. 2016) or natural regeneration (Uriarte and Chazdon 2016). There is a necessity to consider this practice as an option where the availability of seedlings is limited to address this very large forest restoration requirement and to provide a low cost option to shape degraded landscapes with desired tree species that creates a biodiverse forest ecosystem.

There have been several reviews on direct seeding of regional character (Douglas et al. 2007 – pastoral land in New Zealand; Schmidt 2008 – tropical forests; Peppin et al. 2010 – post-fire in western US; Pandey and Prakash 2014 – tropical dry forests), focused on few species (Dey and Buchanan 1995; Farlee 2013), focused on one perspective (Ceccon et al. 2016 – meta-analysis), or from an ecological perspective primarily examining tropical forest species (Ruiz-Jaen and Aide 2005; Pamela and Laurance 2015). This review contributes to the discussion by examining the field performance of direct seeding in forest restoration programs from a number of perspectives. The objective of this review is fivefold: 1) to examine the merits of direct seeding, 2) explore current research findings from a biological perspective across temperate and tropical forest species, 3) to evaluate responses to operational silvicultural practices, 4) to examine potential new application practices, and 5) to provide a synthesis of what is currently known about direct seeding practices so practitioners can make rational decisions on whether to apply this practice in their forest restoration program.

2 Merits of Direct Seeding as a Reforestation Option

2.1 Ecological

Under certain conditions there is a shift in the objective of establishing a new forest to a more ecological approach (species mixture, close to nature appearance and ecological based management). This approach has been defined as ecological restoration which "…is an intentional activity that initiates or accelerates recovery of an ecosystem with respect to health, integrity and sustainability." (SER 2002). Facing ambitious plans for forest restoration at global level, it is imperative to use the most suitable establishment technique directed at both ecological and economic aspects of the process. Forest restoration can restore many ecosystem functions and recover many components of the original biodiversity (Chazdon 2008). Thus direct seeding is suitable for ecological restoration with multiple species because it is easier to create species mixtures compared to planting (Schmidt 2008; Pandey and Prakash 2014), which have greater diversity at higher plant densities and are less expensive to implement than traditional seedling planting techniques.

Direct seeding, along with cover crops and/or nurse trees, has been considered a viable alternative to achieve a more "close-to-nature" silviculture option for site restoration (Madsen et al. 2016). In a review of projects in Brazil direct seeding with many species provided better species diversity in many site restoration programs compared with "passive restoration" (Brancalion et al. 2016). For example in a restoration project in the Brazilian dry forest, direct seeding or planting of seedlings increased the species richness compared to natural regeneration (Figure 1A). In other examples, direct seeding and planting of sites with multiple species initiated in the development of complex Amazonian forest ecosystem (Parrotta and Knowles 1999 and 2001) and the establishment of a mixture of Acacia species (and other genera) as potential hosts for *Santalum spicatum* (Woodal and Robinson 2002). In another Brazillian restoration project (Campos-Filho et al. 2014), a mixture called *muvuca*, consisting of native trees (200,000 seeds ha^{-1}), annual and subperennial legumes (100,000 seeds ha^{-1}), and sand, was direct seeded by common agricultural machinery at the rate of 60 kg ha^{-1}. This approach results in a multilayer vegetation complex, and six years after seeding a mean density of 7,250 trees ha^{-1}, compared to 1,666 trees ha^{-1} in a seedling planting program. However, these very high direct seeding rates are required because tree seedling establishment rates are low (ranging from 1% to 16%) (Campos-Filho et al. 2014); which are comparable to or lower than establishment rates reported for other tropical species (Table 2a). These examples support the view that successful direct seeding (sans planting) is a restoration strategy to restore biodiversity of degraded tropical forests (Lamb et al. 2005). Direct seeding is considered a viable option in ecological orientated restoration programs because, compared to natural regeneration, it allows for greater control of species composition and stocking levels on restored sites (Stanturf et al. 2014).

Direct seeding, like the planting of seedlings, has the potential to initiate a mixed structure stand. For example, it can create variable seed distribution (Figure 1B) and a wide size range of established seedlings (Figure 1C), to create non-uniform forest stands. In certain cases the creation of complex, rather than uniform, forest stands with diversity of stand structures is considered a desirable pathway to ecological forest restoration (Oliver et al. 2016).

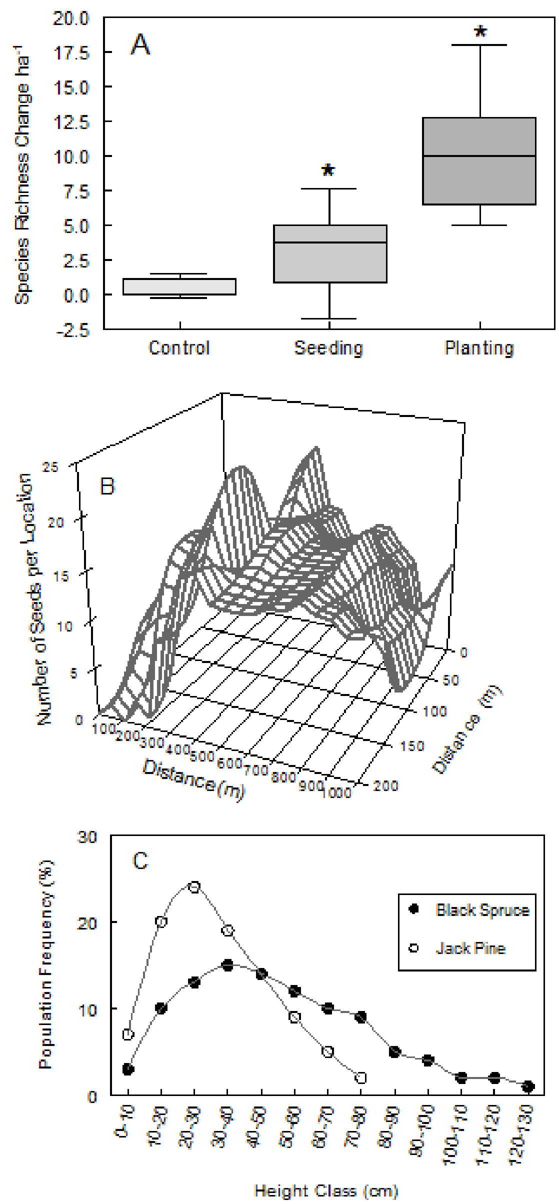

Figure 1. A) Changes of species richness between initial and final measurements (* indicates treatments are significantly different based on a Tukey test *p*= 0.05) for restoration treatments direct seeding and seedling planting in relation to a control site (average initial species richness of 18 with a range of 11-26) in the Brazilian Deciduous forest region (adapted from Sampaio et al. 2007), B) Distribution of seeds collected from an aerial seeded program for *Enterolobium cyclocarpum* across a restoration site (adapted from Garcia Cuevas et al. 2010), and C) Seedling height frequency distribution of direct seed sites for *Picea mariana* after ten years (adapted from Groot 1996) and *Pinus banksiana*) after three years (adapted from Foreman 1997).

Enrichment seeding of late successional species in established forests is considered a potential restoration strategy to increase species diversity at a low cost (Holl and Aide 2011). Direct seeding of late successional hardwood species under conifer plantations to create more diverse forest stands has had modest success because seedling establishment rates are low (i.e. ~13%) (Balandier and Prévosto 2016) or growth is less than planted seedlings (Ammer and Mosandl 2007). Active methods of ecological restoration require that site-adapted seed material be sown in the outplanting window when site environmental conditions are suitable for seedling establishment (Stanturf 2016). Thus issues related to successful stand establishment still need to be considered (see Direct Seeding Field Performance section) because not all direct seeding programs are successful (Peppin et al. 2010), making this a uncertain ecological restoration option in late successional forests.

2.2 Biological – Root System Form

Direct seeding is perceived to produce field-grown plants that have a more natural root system compared to planted seedlings (Ammer and Mosandl 2007). Trials found that seeded-in-place root systems typically have an open and unrestricted pattern with either tap roots or lateral roots radiating from the root collar (Little and Somes 1964; Sutton 1969; Long 1978; Preisig et al. 1979; Van Eerden 1982). However, this pattern is not universal because seedlings originating from seed can also have poorly formed root systems (Harrington et al. 1989). Bareroot and container-grown seedlings initially take on a different root form because these stocktypes' root form is, in part, dictated by nursery cultural and planting practices (reviewed by Grossnickle and El-Kassaby 2016).

Differences in root form between direct seeded seedlings and planted seedlings are still considered an issue in developing current restoration programs (e.g. Fischer et al. 2016). This concern stems from the fact that a number of studies reported newly established planted seedlings/saplings had shoot system stability issues (Nichols and Alm 1983; Halter et al. 1993; Balisky et al. 1995; Wennström et al. 1999). However, this concern is not always apparent. For example, belowground root development patterns of *Pinus radiata* did not differ between direct seeded and planted seedlings, with the potential for toppling related to shoot biomass allocation (Waston and Thombleson 2002). Even though there is a planted seedling stocktype effect on long-term root development patterns, inherent species characteristics and site environmental and soil physical factors also shape root system form as seedlings/saplings grow into an established forest stand (Sutton 1969). Root distribution, tree stability and stem straightness of planted seedlings can develop over time a similar form of trees regenerated from seed (Grossnickle and El-Kassaby 2016).

2.3 Economic

Direct seeding is considered a viable regeneration option because it is cheaper than planting seedlings (Smith 1962; Jõgiste et al. 2016). Direct seeding avoids all costs involved in planting seedlings (i.e. reduced labor, less equipment, no nursery and limited handling costs, and minimal operational plans). If one just defines reforestation success as 'putting the plant material for the next forest stand into the ground', then direct seeding costs are considerably lower than planting seedlings.

Table 1. Cost comparison between direct seeding and planting seedlings for various forest restoration programs. The cost comparison ratios between direct seeding and either container-grown or bareroot seedlings was calculated for a density of 2,500 seedlings ha^{-1}.

Species	Prices ha^{-1}					RATIO[3]			SOURCE
		Container							
	Direct Seeding	Manual	Mechanical	Bareroot [1]	**Currency**[2]	DS/CON Man	DS/CON Mech	DS/BR	
Multiple species in Australia	1,121	6,913	5,420		AUS	16%	21%		Summers et al. 2015
Pinus contorta	365			1,280	CAN			28%	Caldicott 1989 (converted to 2500 seedlings per ha)
Pinus contorta	249			772	US			32%	Sullivan and Sullivan 1984
Pseudotsuga menziesii	303			772	US			39%	
Pinus sylvestris	450	1,000			Euro	45%			Helenius 2016
Quercus robur	1,375			3,000	Euro			46%	Madsen and Löf 2005
Quercus sp.	845	1,200			Euro	70%			González-Rodríguez et al. 2011
Betula sp.	245			1,415	UK			17%	Willoughby et al. 2007
Five species in Costa Rica	351			3,737	AUS			9%	Cole et al. 2011 (converted to 2500 seedlings per ha)
Five species in Brasil	830			1,850	US			45%	Engel and Parrotta 2001
New Zealand native species	9,610			18,745	NZ			51%	Douglas et al. 2007
Quercus sp.	64			150	US			42%	Bullard et al. 1992
Fagus sylvatica and *Abies alba*	900			6,600	US			14%	Baumhauer et al. 2005
Fagus sylvatica	700			3,750	Euro			19%	Madsen et al. 2006
Fagus sylvatica	2,000			7,000	Euro			28%	Birkedal et al. 2006
Pinus kesiya	339			2,050	PhP			16%	Noble 1985
Pinus banksiana	210	717			US	29%			Adams et al. 2005
Picea mariana	216	780			US	28%			Adams et al. 2005
AVERAGE RATIO						**38%**	**21%**	**30%**	

1) Stocktype trial information was defined as bareroot seedlings when there was clear definition of stocktype type.
2) Currency: Australian dollar (AUS), United States dollar (US), Canadian dollar (CAN), Euro (EU), United Kingdom pound (UK), New Zealand dollar (NZ)
3) DS – direct seeding, Cman – manual planting of container seedlings, Cmech – mechanized planting of container seedlings.

A review of studies comparing costs between direct seeding and planting found the average cost of direct seeding per hectare was 30% to 38% (ranging from 9% to 51%) of planting costs for planting of bareroot and container-grown seedlings (Table 1); with the cost ratio, strongly dependent on seed price and seeding rate. Other economic analyses have also found that it can cost from 40% (Bullard et al. 1992; Duryea 1992; Campos-Filho et al. 2014) to 50% (Schultz 1997; Thomson 2007; Matute and Mitchell 2015) the cost of planting seedlings. Direct seeding was up to 29 times more cost effective than planting container stock when considering base costs, though it resulted in lower establishment success compared to container-grown seedlings (Palmerlee and Young 2010). However, in some cases high seed price and seeding rate, result in direct seeding costing more than planting (i.e. seeding of 100,000 acorns ha^{-1} costs 175% of the price for planting 2,500 oak seedlings ha^{-1} – Willoughby et al. 2004).

However, successful forest restoration is a comprehensive process. During the initial stages of forest regeneration, a series of intensive nursery or seed preparation, and silviculture practices are required to ensure successful seedling establishment (Gladstone and Ledig 1990; Grossnickle 2000). Ultimately, any determination of forest regeneration success needs to consider all costs that are required to achieve a fully established forest stand. These costs include 1) Species and genetic source selection, 2) Seed collecting and processing, 3) Site modifications and seedbed preparation, 4) Seeding, 5) Vegetation and predation control, and 6) Re-seeding and thinning. Potential failure can occur from direct seeding if preparation of the site and the protection of newly established seedlings are not consider part of a comprehensive plan (Toumey 1916; Balandier and Prévosto 2016).

2.4 Operational

Direct seeding needs to be compared to conventional seedling planting programs to determine when it is a viable operational option. The following is a list of operational reasons for using direct seeding in a restoration program (Toumey 1916; Smith 1962; Herman 1978; Barnett and Baker 1991; Owston et al. 1992; Fleming et al. 2001; Ochsner 2001; Schmidt 2008; Ezell 2012; Barnett 2014).

- Rapid reforestation of large areas which result from wildfire or other natural disasters.
- Rapid restoration after a disturbance to give the desired tree species an opportunity to reestablish the site before development of competing vegetation.
- Provides a 'shortcut' alternative to implement the planting step of a restoration program.
- Planting of remote or inaccessible sites or sites with rocky soils making it difficult to plant seedlings.
- A viable restoration option where there is a limited availability of bareroot or container-grown seedlings.
- Enrichment planting in secondary forests.
- Restoration of disturbed areas where natural regeneration is not adequate.
- Afforestation option for large abandoned agricultural sites and mine reclamation projects.
- Application in agroforestry situations for rapid control of site resources away from weed species and directed towards the agricultural crop and tree species.
- Use on low-productive or disturbed sites where the cost of planting operations is not economically feasible.
- Use in low-budget restoration programs addressing conservation and recovery of forest ecosystems.

Direct seeding is a 'more simplified regeneration practice' because it avoids relatively complicated nursery, handling and planting phases. However, direct seeding requires substantial quantities of seeds to sufficiently stock the field sites (see - Recommended Seeding Rates section). Direct seeding requires less labour, and can be mechanized (e.g. drilling and aerial seeding). This simplified silvicultural operation could be critical for restoring up to two billion hectares of forest sites worldwide (Minnemayer et al. 2011).

Silvicultural practices that are part of an overall restoration program (e.g. vegetation control and surveys to define stand establishment success) are affected by whether the site is established via direct seedling or seedling planting. During the establishment phase, directly seeded seedlings are much smaller compared to planted seedlings (see - Direct Seeding versus Seedling Comparison section), which complicates vegetation control (see - Competitive Vegetation section). In addition, direct seeding creates an irregular pattern of seedlings, thereby limiting systematic mechanized vegetation control. Two or three assessments of establishment success are typically required after direct seeding because of delayed seedling establishment (Barnett 2014). Thus, silvicultural practices need to be modified to integrate a direct seeding program into the overall forest regeneration process.

3 Current Direct Seeding Research

The following discussion provides a review of 75 direct seeding trials from the past 25 years. This represents a comprehensive, though not exhaustive, examination of recently published literature for tropical (Table 2a), temperate hardwood (Table 2b) and conifer (Table 2c) tree species and describing major trends.

3.1 Conversion Rates

Germination Rate – The overall average germination rate for direct seeding was 44% and ranged from 9% to 92%. The average germination rate was 38% for tropical species, 47% for temperate hardwoods and 46% for temperate conifers.

Establishment Rate – (survival rate after at least one growing season per / total number of seeds planted) - The establishment rate across all studies was 21% ranging from 0% to 92%. The average establishment rate was 17% for tropical species, 28% for temperate hardwoods and 16% for temperate conifers.

These findings show that, in general, direct seeding programs result in a low rate of initial stand establishment. Other reviews also have shown low seedling establishment rates with direct seeding on restoration sites (Pamela and Laurance 2015; Ceccon et al. 2016). Historically, reasons for low establishment rates are timing of seeding (Wendel 1971; Ledgard 1976), planting practices (Wendel 1971), microsite environment (Show 1924; Wahlenberg 1925; Wendel 1971; Ledgard 1976), competitive vegetation (Fraser 1981) and seed predation (Show 1924; Wahlenberg 1925). These factors interact together to result in low seedling establishment rates. For example, Lawrence and Rediske (1962) found that seed losses occurred throughout the first year, due to various factors, as seeds go through the germination process and attempt to grow into an established seedling (Figure 2).

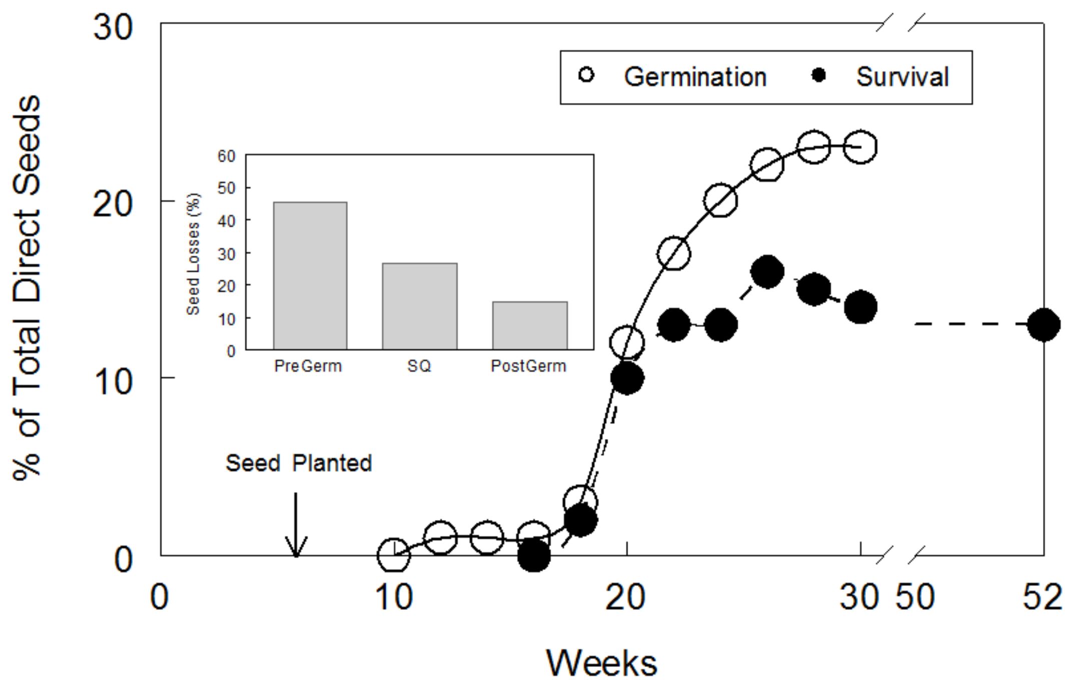

Figure 2. Germination and survival of *Pseudotsuga menziesii* var. *menziesii* seedlings in a direct seeding trial on a scarified reforestation site during one year. Insert figure shows where seed losses occurred during the trial: pre germination (PreGerm –losses primarily from molds, insects, rodents and birds), seed quality (SQ –due to empty, moldy or quality seed that did not germinate), or post germination (PostGerm –due to fungi or environment [frost or desiccation]) (adapted from Lawrence and Rediske 1962).

To achieve a successful direct seeding program, several factors must be considered. Toumey (1916) listed these factors as 1) tree species and seed quality, 2) timing of seeding, 3) depth of covering (i.e. planting practices), 4) soil conditions (i.e. microsite environment), 5) vegetative cover, and 6) seed predation. As noted above, these are the same factors associated with reduced conversion rates. Along with the quantity of seed sown (see Direct Seedling – Recommended Seeding Rates section), some combination of these factors determine whether direct seeded material successfully goes through the three main stages in the establishment of direct seedling; which are germination, establishment during the first growing season, and survival and growth over the first couple of years. In current published work these controlling factors are still important for direct seeding success as discussed in the following sections.

Table 2a. Direct seeding field performance of tropical forest species.

Species	Site Type	Germination rate	Establishment	Reference
Borneo rain forest species *Ficus stupenda*	Reforestation		0%	Laman 1995
Pioneer rainforest species *Alphitonia petriei*	Reforestation		7%	Sun et al. 1995
	Reforestation - Weed Control		27%	
9 native species to Puerto Rico forests	Afforestation	32%	18%	Zimmerman et al. 2000
	Reforestation site - Weed Control	17%	10%	
5 native tree species to the Amazon Basin	Reforestation	10%	5%	Engel and Parrotta 2001
6 native tree species to Hawaii	Reforestation - Multiple		3%	Cabin et al. 2002
11 native tree species to the Amazon Basin	Bare Soil		33%	Camargo et al. 2002
	Pasture		23%	
	Secondary Forest		15%	
	Mature Forest		12%	
20 native tree species to Panama Tropical Forests	Reforestation -Shaded		19%	Hooper et al. 2002
	Reforestation - Mowed/Sun		9%	
3 native Malaysian Tropical forest species	Reforestation		5%	Howlett and Davidson 2003
Swietenia macrophylla	Reforestation - Buried		9%	Negreros-Castillo et al. 2003
	Reforestation - Surface		4%	
Australian Tropical Forest Species	Reforestation - Broadcast		4%	Doust et al. 2006
	Reforestation - Buried		28%	
Eight Indian tropical dry forest specis	Afforestation		30%	Singh and Singh 2006
Mixed species in Hawaiian Dry Forest Ecosystem	Reforestation with herbicides		3%	Brooks et al. 2009
Enterolobium cyclocarpum	Reforestation		22%	Garcia Cuevas et al. 2009
Three tree species in the semi-evergreen forest - Yucatan Peninsula, Mexico	Recently abandoned (<5 years)		7%	Bonilla-Moheno and Holl 2010
	Young successional forest (8–15 years)		16%	
	Established forest (>50 years)		21%	
Keteleeria evelyniana	Afforestation - Buried		42%	Sovu et al. 2010
	Afforestation - Broadcast		13%	
Schima wallichii			14%	
Pinus kesiya			38%	
Tropical montane forest	Tree plantation	43%	32%	Cole et al. 2011
	Pasture	43%	18%	
	Secondary forest	43%	19%	
Seeds of 19 indigenous lowland tropical forest tree species from Thailand	Seed Size - Small		5%	Tunjai and Elliott 2011
	Seeds Size - Medium		18%	
	Seed Size - Large		40%	
Indigenous tree species of China	Vegetation		10%	Wang et al. 2011
	Vegetation Removal		14%	
Brosimum alicastrum		75%	44%	Laborde and Corrales-Ferrayola 2012
Enterolobium cyclocarpum		60%	13%	

Table 2a. Direct seeding field performance of tropical forest species – Continuation.

Species	Site Type	Germination rate	Establishment	Reference
Four species in Hawaiian Dry Forest Ecosystem	Afforestation - Mowed		0%	Ammondt et al. 2013
12 tree species in the Brazilian deciduous and semideciduous forests	Afforestation - grass canopy	29%		de Souza Gomes Guarino and Scariot 2014
	Afforestation -no grass canopy	20%		
Afzelia xylocarpa	Afforestation		44%	Hossain et al. 2014
Eugenia cumini			10%	
Ficus racemosa			5%	
Gmelina arborea			5%	
Schleichera oleosa			40%	
Six Brazilian savanna species	Afforestation	52%	34%	Silva et al. 2015
Oreomunnea mexicana subsp. mexicana	Secondary forest	37%	7%	Atondo-Bueno et al. 2016
	Average	**38%**	**17%**	

Common names were provided in some instances because the appropriate scientific names were not provided in the cited reference.

Table 2b. Direct seeding field performance of temperate hardwood species.

Species	Site Type	Germination rate	Establishment	Reference
Quercus shumardii and *Quercus phellos*	Reforestation		35%	Wittwer 1991
Acacia sophorae	Afforestation		6%	Barron and Dalton 1996
Eucalyptus dioersifolia			0%	
Quercus pagoda	Reforestation		78%	Stanturf and Kennedy 1996
Quercus rubra	Under planted in plantation		50%	Trencia 1996
Quercus rubra	Reforestation		53%	Zaczek et al. 1997
Bottomland Forest Species	Reforestation	35%		Stanturf et al. 1998
Quercus nuffallii	Afforestation		15%	Schweitzer and Stanturf 1999
Quercus rubra	Reforestation - Multiple		29%	Parker et al. 2001
Fagus sylvatica	Reforestation - Multiple		23%	Ammer et al. 2002
Bottomland Forest Oaks	Reforestation		22%	Twedt and Wilson 2002
Quercus liaotungensis	Reforestation site - Large gap	60%	48%	Li and Ma 2003
	Reforestation - Small gap	50%	40%	
	Reforestation - Understory	43%	32%	
Carya cordiformis, *Betula alleghaniensis*, *Fagus grandifolia*, and *Juglans nigra*	Uncolanized Woodlots		1%	Hewitt and Kellman 2004
Northofagus solandri var. cliffortioides	Reforestation		1%	Ledgard and Davis 2004
Leptospermum scoparium			1%	

Table 2b. Direct seeding field performance of temperate hardwood species - Continuation.

Species	Site Type	Germination rate	Establishment rate	Reference
Operational planting of multiple hardwood species in the United Kingdom	Afforestation - Multiple		10%	Willoughby et al. 2004
Quercus petraea - Fenced for herbivore control (Y/N)	Control (Y)		56%	
	Cover Crop (Y)		58%	
	Weed Free (Y)		60%	
	Weed Free (N)		51%	
Quercus robur	Reforestation (4 years)		50%	Madsen and Löf 2005
	Reforestation (4 years)		23%	
Fraxinus excelsior	Reforestation	30%	21%	Jinks et al. 2006
Acer pseudoplatanus	Reforestation	30%	27%	
Eucalyptus marginata	Afforestation		10%	Koch and Samsa 2007
Quercus castaneifolia	Site Fertility - low	90%	36%	Tabari and Asri 2008
	Site Fertility - medium	90%	43%	
	Site Fertility - high	90%	65%	
Quercus macrocarpa	Reforestation	56%	56%	Lalibert´e et al. 2008
Quercus robur		92%	92%	
Twelve native woody species in New Zealand	Afforestation - Multiple		10%	Ledgard et al. 2008
Quercus robur	With Tree Shelters		56%	Valkonen 2008
Quercus ilex	Reforestation site _ Multiple	45%	29%	Mendozza et al. 2009
Quercus pyrenaica		41%	26%	
Acer granatense		9%	4%	
Sorbus ariea		19%	9%	
Quercus nuttallii	Afforestation		12%	Stanturf et al. 2009
Mixed species in lowland British forest	Reforestation		20%	Willoughby and Jinks 2009
	Reforestation site with herbicides		40%	
Quercus palustris	Reforestation site - Multiple		10%	Motsinger et al. 2010
Quercus ilex	Afforestation		12%	González-Rodríguez et al. 2011
Quercus suber			22%	
Populus fremontii	Reforestation		7%	Grabau et al. 2011
Salix gooddingii			1%	
Betula pendula and *B. pubescence*	Reforestation		31%	Rouvinen and Koulki 2011
Quercus robur	Afforestation		53%	St Denis et al. 2013
Acer saccharum			3%	
Nine Austrailian pioneer tree species	Restoration - Multiple		1%	Florentine et al. 2013
Prunus pensylvanica	Afforestation	4%	3%	Smreciu and Gould 2015
Prunus virginiana		12%	8%	
	Average	**47%**	**28%**	

Common names were provided in some instances because the appropriate scientific names were not provided in the cited reference

Table 2c. Direct seeding field performance of temperate conifer species.

Species	Site Type	Germination rate	Establishment	Reference
Pinus taeda	Reforestation	12%	3%	Huebschmann and Wittwer 1992
Picea mariana	Reforestation		35%	Groot and Adams 1994
Pinus sylvestris	Reforestation	42%	34%	Winsa and Bergsten 1994
	Reforestation	63%	52%	
Picea mariana	Reforestation - Mineral/humus interface		8%	Fleming and Mossa 1994
	Reforestation - Surface		1%	
Picea mariana	Reforestation - Litter seedbed		2%	Fleming and Mossa 1995
	Reforestation - Thin organic matter seedbed		23%	
	Reforestation - Shallow mineral seedbed		20%	
Picea glauca	Reforestation - Mound seedbed		6%	DeLong et al. 1997
	Reforestation - Rotten log seedbed		7%	
	Reforestation - Exposed seedbed		11%	
	Reforestation - Normal seedbed		5%	
	Reforestation - Screef seedbed		7%	
Pseudotusuga	Reforestation - VEG - None		34%	Caccia and Ballaré 1998
menziesii	Reforestation - VEG - Medium		30%	
	Reforestation - VEG - High		10%	
Abies balsamea	Conifer forest	30%	12%	Cornett et al. 1998
Pinus strobus		36%	8%	
Pinus sylvestris	Reforestation - No site preparation		10%	Wennström et al. 1999
	Reforestation - Microsite preparation		15%	
Picea glauca	Reforestation	28%	15%	Stewart et al. 2000
Pinus sylvestris	Reforestation	88%	45%	de Chantal et al. 2004
Picea abies		72%	17%	
Pinus sylvestris	Reforestation			Nilson and Hjältén 2003
	Open	73%	9%	
	Closed canopy	60%	15%	
Pinus sylvestris	Afforestation - Fenced for herbivore control	(Y/N)		Willoughby et al. 2004
	Control (Y)		4%	
	Cover Crop (Y)		5%	
	Weed Free (Y)		9%	
	Weed Free (N)		0%	
Pinus sylvestris	Reforestation - Stand Seed		38%	Wennström et al. 2007
	Reforestation - Orchard Seed		43%	
Pinus sylvestris	Reforestation - Multiple	26%	6%	Erefur et al. 2008
Picea abies		27%	7%	
Picea mariana	Reforestation		17%	Gauthier and Ruel 2008
Pinus sylvestris	Reforestation	55%	1%	Mendozza et al. 2009
Pinus kesiya	Reforestation		38%	Sovu et al. 2010
Pinus resinosa	Afforestation		6%	St Denis et al. 2013
Thuja plicata	Reforestation	31%	0%	Sheridan et al. 2016
	Average	**46%**	**16%**	

3.2 Factors Affecting Conversion Rates

Seed Parameters

Knowing which tree species have suitable characteristics for direct seeding is critical to the success of forest restoration projects that rely on direct seeding (Tunjai and Elliott 2011). In general, species used for direct seeding must be stress tolerant, have fast germination, establishment and initial growth, and a certain degree of shade tolerance (Schmidt 2008), though site conditions will dictate the selection of tree species and seed source. Local seed sources of early-successional and pioneer species, with their ability to grow rapidly, and late-successional and climax tree species with large seeds and food reserves (Piggott et al. 1987; Pandey and Prakash 2014) can be successfully established. Population size and the initial genetic diversity of trees selected for seed collection can have strong effects on seed quality, germination and survival, which affects genetic diversity in future generations (Ivetić et al. 2016b). To maintain a high level of genetic diversity in the new forests, the use of reproductive material originating from well-designed seed orchards, the use of seed mixtures from different seed sources and provenances, and the use of seed collected from trees of different ages are recommended (Ivetić and Devetaković 2016b, 2017).

Poor seed germination rates (Holl et al. 2000; Engel and Parrotta 2001) or small seed size (i.e. smaller seeds performed poorly) (Camargo et al. 2002; Hooper et al. 2002; Doust et al. 2006 and 2008; González-Rodríguez et al. 2011) have resulted in low establishment rates. Large seeded species (Hooper et al. 2002; Birkedal 2010; Tunjai and Elliott 2011; St-Denis et al. 2013) and greater seed weights tend to result in better germination (Zimmerman et al. 2000; de Souza Gomes Guarino and Scariot 2014) and establishment rates (Camargo et al. 2002; Hooper et al. 2002; Doust et al. 2006; Wang et al. 2011; Hossain et al. 2014). Stanturf and associates (1998) found that only heavy-seeded species of *Quercus* spp. and *Carya* spp. have the capability to be successfully direct-seeded. In examining all trials that direct seeded temperate hardwoods (Table 2b) the average establishment rate for oak species was 45% compared to only 10% for all other hardwood species. One benefit of large seeds in direct seeding programs is that their larger store of carbohydrates improves seedling establishment (Khurana and Singh 2001).

However, some studies report a weak association between seed weight and germination (de Souza Gomes Guarino and Scarion 2014). This is because other factors such as seed form and moisture content also affect their establishment (Tunjai and Elliott 2011). Small seeds and seeds with low water content have less susceptibility to desiccation in dry regions, and have a comparatively better potential to enter disturbed soil when broadcast seeded (Pandey and Prakash 2014). Seed size along with seeding practice can influence establishment success because seed burial had a negative effect on emergence of flat seed species compared to round seed species (Silva et al. 2017). A number of recent reviews found that, in general, seed size improves subsequent seedling establishment, though not in all situations (Ceccon et al. 2016; Figure 3), making it difficult to make generalized statements related to seed quality and direct seeding success.

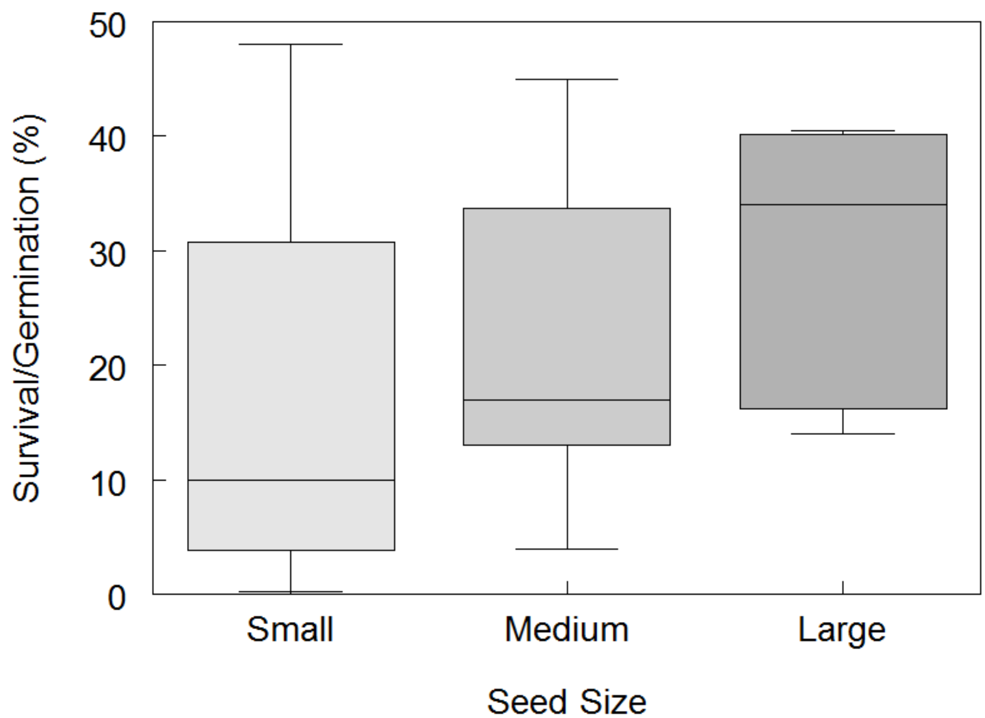

Figure 3. Survival/germination (box plots with median, box out to the 1st and 3rd quarterlies with whiskers to 1.5 times the interquartile range) in relation to seed size (mass) for direct seeding trials where the seed size categories were small (0–99 mg - n = 29) medium (100–2000 mg - n = 14) and large (>2000 mg - n = 6) (adapted from Pamela and Laurence 2015).

Germination speed and seed dormancy also affect seedling establishment rate after direct seeding. There are reports of seed germination occurring in 2 to 4 years after direct seeding, due to seed biology (Löf et al. 2004), or environmental conditions (Petursson and Sigurgeirsson 2004). Species with a weak seed dormancy sown in spring typically emerge after a few months, and species with deep seed dormancy can emerge up to a year later after a long exposure to site conditions (Frochot et al. 2009). Deep dormant seed must be pre-treated before direct seeding (Schmidt 2008), because delayed germination can lead to extended need for vegetation and predation control on restoration sites. Untreated dormant seed allow better flexibility in terms of seeding time, while pretreated seed must be sown when dormancy is broken (Frochot et al. 2009). Thus, knowledge of seed biology is necessary in planning a direct seeding program.

The use of high quality seed is imperative because it increases the early success by improving the establishment rate, and also forest stand performance due to increased genetic gain. Genetic variability of seed can have a significant effect on field performance. For example, seeds of *Pinus sylvestris* from seed orchards increased direct seeded seedling establishment by 41% (Wennström et al. 1999), as well as resulting in taller seedlings four years after seeding compared to seed from natural stands (Wennström et al. 2007). Survival of *Pinus sylvestris* seedlings from direct seeding was improved with better seed quality (Winsa and Bergsten 1994). A cost-benefit analysis showed that, the net cost of *Pinus sylvestris* orchard seed was less than that of natural stand seed, with 7% yield improvement and 15% better seed quality (Ahtikoski and Pulkkinen 2003). Providing enough high-quality seed for direct-seeding programs is an issue because seeding rates are much higher than nursery seeding rates (See Direct Seedling – Recommended Seeding Rates section). One possible solution would be the availability of seeds from seed orchards via low-budget breeding programs (Lindgren 2016).

Timing of Seeding

Seeding should occur when site environmental conditions are least stressful. "Ultimately success will depend on timing emergence so that emergence and survival of seedlings is maximized" (Jinks et al. 2006). The best time for seeding is when they have the best chance of germination; which means plentiful moisture, optimum temperature, minimal weed competition, and a potentially favorable growing season before exposure to stressful environmental conditions (Schmidt 2008). Soil nutrition, while important, is a secondary factor in seed germination and initial seedling establishment. The following examples show that the season to ensure the best seed germination and establishment changes with species and forest ecosystem.

Spring

- Spring seeding of oak acorn generally gave better results than autumn seeding (Madsen and Löf 2005).
- Major southern US pine species were best sown in the spring after seed stratification (Barnett 2014).
- Spring seeding of *Pinus concorta*, *Pinus mugo* and *Alnus viridis* was more successful than autumn seeding except on sites covered with snow throughout the winter (Ledgard 1976).
- Twenty woody species in France favored spring seeding with buried seed (Frochot et al. 2009).
- *Pinus banksiana* stand regeneration was significantly better after spring than fall seeding (Chrosciewicz 1990).
- Spring direct seeding of *Pinus sylvestris* and *Picea abies* resulted in greater seedling establishment (Figure 4) and resulted in larger seedlings after three years compared to summer-sown seeds (de Chantal et al. 2004).

Fall

- Fall planting of oak seeds in Iberian woodlands is recommended because of seasonal rains (Sánchez-González et al. 2016).
- Fall seeding is generally recommended for *Pinus palustris* because their seeds germinate naturally in the fall (Barnett 2014).
- Fall seeding *Spartium junceum* on an afforestation site resulted in successful germination and survival (Brofas and Karetsos 2002).

Winter

- Seeding time was the most significant variable in the Western Australian wheatbelt; with seeds sown in the winter out-performing later seeding times (Piggot et al. 1987).
- Jinks et al. (2006) recommended seeding in late winter for *Fraxinus excelsior* and *Acer pseudoplatanus*, though winter conditions (i.e. waterlogged soils and frost) can limit seedling emergence.

Multiple Seasons

- Temperate hardwoods, in the Lower Mississippi Alluvial Valley, had successful establishment across multiple seasons (i.e. November through June) (Stanturf et al 1998).

Ultimately, timing of direct seeding is dictated by the time of year providing the best chance of maintaining consistently optimum environmental conditions that once seeds germinate, young seedlings avoid planting stress and become established. For example, in the tropical dry forests planting seeds when the soil has sufficient moisture in the rainy season can increase seedling establishment (Vieira and Scariot 2006), while in the northern latitude forests spring season planting is only optimal during years when there is soil moisture (de Chantal et al. 2004). Just like planted seedlings, young seedlings from direct seeding need to grow a root system into the soil to achieve a proper water balance as they become coupled with the hydrologic cycle of the planting site (Burdett 1990; Margolis and Brand 1990; Grossnickle 2005). For example, a two month delay of seedling emergence for direct sown oak resulted in the equivalent of one year's growth reduction; which was attributed to the exposure to dry summer conditions (Löf and Birkedal 2009).

Seeding Practices

Seed burial, versus broadcast seeding, was found to improve establishment rates (Negreros-Castillo et al. 2003; Woods and Elliot 2004; Doust et al. 2006; García-Orth and Martínez-Ramos 2008; Sovu et al. 2010). Broadcast seeding is applied in restoration programs because it has the advantage of covering a large area in an efficient manner as well as providing a means to seed remote areas and difficult terrain (Schmidt 2008). The disadvantage of broadcasting is that seeds lie on the ground, exposing them to harsh environmental conditions and predation (discussed in following sections), which can result in very low establishment rates (Ledgard and Davis 2004; Ammondt et al. 2013; Florentine et al. 2013). However, broadcast seeding when combined with proper site and seedbed preparation and vegetation control can be a successful practice (Brooks et al. 2009).

Site preparation techniques that improved the seedbed (i.e. remove competition and create seeding spots near the mineral soil - humus interface) can increase seed germination and seedling establishment (Loewenstein and Pitkin 1966; Fleming and Mossa 1994; Wennström et al. 1999; Oleskog and Sahlén 2000; Hille and den Ouden 2004; Ledgard et al. 2008; Birkedal et al. 2010). Corenett et al. (1998) found reduction in thickness of the forest floor organic layer beneficial for direct seeding of *Abies balsamea* but not *Pinus strobus.* Direct seeding of *Pinus sylvestris* and *Picea abies* resulted in greater seedling establishment when soil scarification exposed seeds to the Ae-B Horizon (Figure 4). Seeding immediately after the site preparation treatment is best because the receptivity of the seedbed declines with the passing of each growing season (Fleming and Mossa 1995). Interestingly, the combination of soil scarification and a dense shelterwood system (300 stems ha-[1]) resulted in higher survival of direct seeded *Picea stichensis* (Farrelly et al. 2003), indicating that managing the entire environment of the restoration site can be critical for ensuring successful establishment.

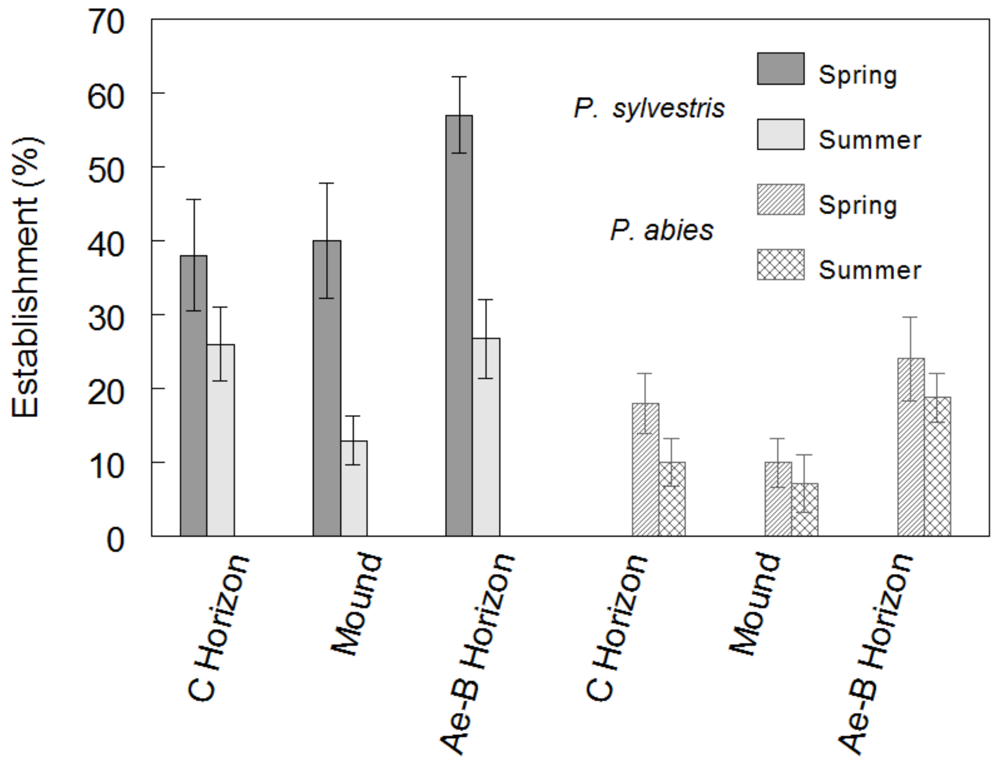

Figure 4. Third year establishment (mean +/- SE) of direct seeded *Pinus sylvestris* and *Picea abies* in relation to planting season and site preparation treatment (i.e. Exposed C Horizon, Mound, or Exposed Ae-B Horizon) after being planted during a moist growing season on a clearcut reforestation site (adapted from de Chantal et al. 2004).

Spot seeding has long been considered a direct seeding option (Toumey 1916). Seeds are usually sown in spots prepared by raking, hoeing, or kicking areas free of vegetation and litter (Barnett 2014). However, ploughed furrows, or scalps to mineral soil, are also effective site preparation techniques to create seeding spots (Stiell 1959). Tractor-mounted seeders have been used and usually result in seeds sown in rows (Schmidt 2008; Barnett 2014). Spot seeding was far more successful than broadcast seeding in conversion of hardwood stands on poor sites for *Pinus strobus* (Wendel 1971), while mechanized seeding of *Pinus sylvestris* produced better results than manual seeding (Kankaanhuhta et al. 2009).

Covering seeds to the proper planting depth enhances seeding results (Nilsson et al. 1996; Li and Ma 2003; Negreros-Castillo et al. 2003; Nilson and Hjältén 2003; Doust et al. 2006; Sovu et al. 2010). Typically the best seeding depth depends on seed size. A general rule is that seeding depth is between one and two times the seed width. This observation is supported by nursery experiments that indicated depth of seeding requirements for a range of native species depending on their seed size: large seeded trees and shrubs, particularly *Acacia spp*. and *Eucalyptus calophylla*, required soil covering of 5-10 mm, while smaller-seeded *Eucalyptus spp*. performed best with a soil covering of 2-5 mm, although good results were achieved for some species by surface seeding (Piggot et al. 1987). Seeding oak seeds from 2.5 to 15 cm deep is recommended depending on acorn size (Johnson and Krinard 1985), with deeper seeding beneficial if soil drying or rodent damage are likely (Stanturf et al. 1998; Oliet et al. 2015). However, soil-buried seeds do not always attain higher germination rates than surface seeding (Pandey and Prakash 2014). In dry tropical forests buried seeds did not have higher germination than broadcast seeds as long as a grass cover provided safety from seed predators and a suitable microclimate with soil moisture similar to the forest (de Souza Gomes Guarino and Scariot 2014). Though there are general rules for proper planting depth, there is enough inconsistency to show that species and site conditions ultimately dictate seeding practices.

Microsite Conditions

Direct seeding success is primarily related to site conditions that make soil water available during the germination and establishment phases (Laman 1995; Knight et al 1997; Stanturf et al. 1998; Oleskog and Sahlén 2000; Engel and Parrotta 2001; Ammer et al. 2002; Chantal et al. 2003; Pausas et al 2004; Woods and Elliot 2004; Jinks et al. 2006; Dodd and Power 2007; Gauthier and Ruel 2008; Laliberté et al. 2008; Mendoza et al 2009; Bonilla-Moheno and Holl 2010; Wang et al. 2011; Florentine et al; 2013; Atondo-Bueno et al. 2016; Helenius 2016). For example, the probability of seedling emergence for *Oreomunnea mexicacana* was directly related to soil water availability with seedling emergence increasing with more available soil water (Figure 5A), though flood prone sites require practices that enhance soil drainage (Gardiner et al. 2004). In a study examining seedling establishment based on location of planting in the soil profile, establishment success was best as soil water availability increased to an optimum level, with the actual best location in the profile changing as soil water status changed (Fleming and Mossa 1989). In a study confirming these observations, the performance of direct seeded *Pinus sylvestris* and *Picea abies* (data from over thirteen thousand operative forest regeneration quality management inventory sites), soil water (along with site preparation and the seeding into mineral soil) was the primary factor(s) affecting direct seeding success (Kankaanhuhta et al. 2009).

The availability of soil water is affected by soil type where direct seeding is applied and the best establishment rate typically occurs on bare mineral soil (Riley 1973; Wittwer 1991; DeLong et al. 1997; Knight et al. 1997; Caccia and Ballaré 1998; Carmargo et al. 2002; Hanssen 2002; de Chantal et al. 2005; Madsen and Löf 2005; Stevenson and Smale 2005) where removing the organic soil layer improves continuous water availability which is critical for germinating seeds (Hille and den Ouden 2004). The recommended seedbed for best seedling establishment from direct seeding in northern latitude forests is reported to be mineral soils that are still "fresh"; meaning the disturbed soil has not had time to settle, thereby providing spaces where seeds can settle before the soil becomes compacted with plentiful, but not excessive soil water and moderate temperature conditions (~10 – 25 ^{o}C); with nutrition not a noted concern (Fleming et al. 2001). However, there are exceptions to planting in mineral soil. For example, poorly decomposed *Sphagnum* peat was the best seedbed for black spruce

(Groot 1994); a species typically found on wet low lying northern latitude forest bog sites (Harlow and Harrar 1969). Though mineral soils are a preferential seedbed, in northern latitude forests, seeds planted in open sites can incur injury and/or mortality due to frost heaving (Erefur et al. 2008), indicating that site selection for direct seeding needs to consider conditions across all seasons.

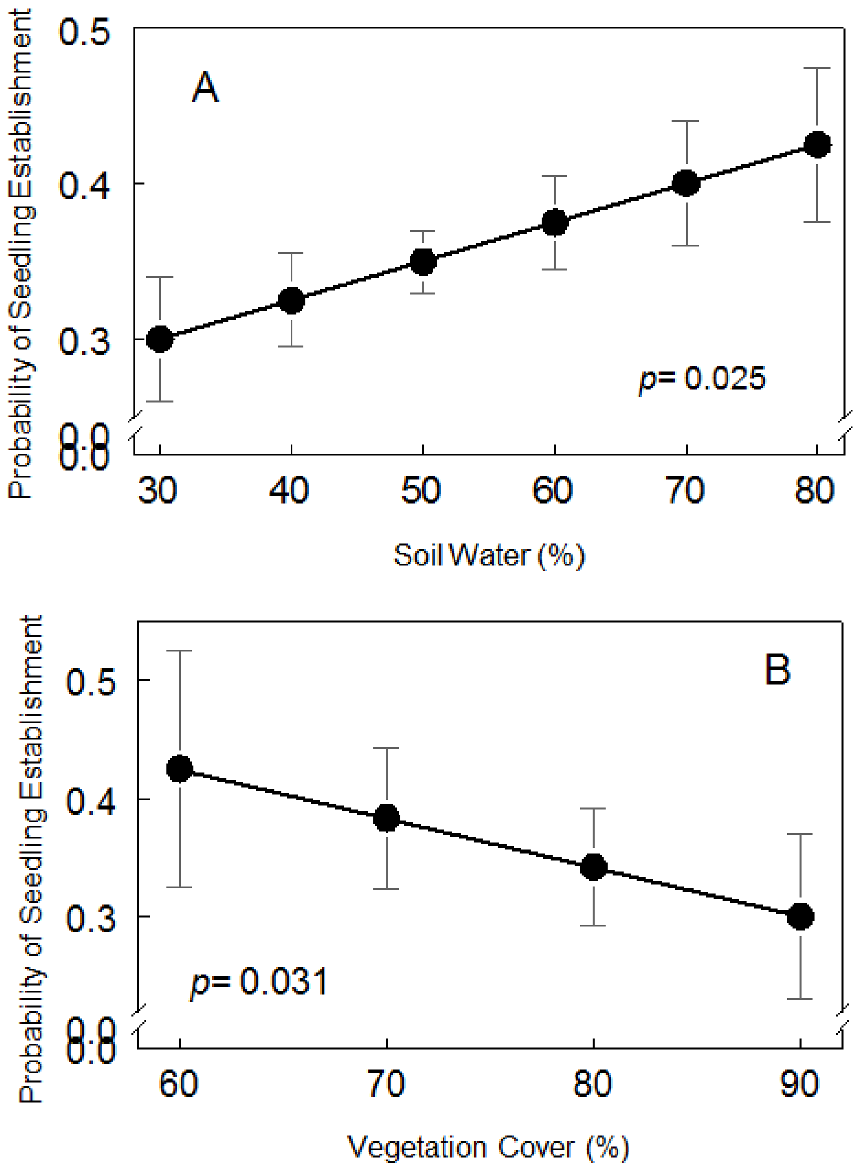

Figure 5. Probability of seedling establishment from direct seeding of *Oreomennea mexicana* under field conditions in relation to site soil water content (A) and vegetation cover (B) (adapted from Antondo-Bueno et al. 2016). Note: Bars through data points represent the 95% confidence interval.

Competitive Vegetation

Competition for site resources is one of the major factors limiting the successful establishment and growth of seedlings (Gjerstad et al. 1984; Sutton 1985; Radosevich and Osteryoung 1987; Grossnickle 2000). For example, the probability of seedling emergence for *Oreomunnea mexicacana* decreased with greater vegetation cover (Figure 5B). Competition from site vegetation has resulted in low conversion rates in direct seeded programs (Winsa and Bergsten 1994; Sun et al. 1995; Knight et al. 1997; Cornett et al. 1998; Holl et al. 2000; Engel and Parrotta 2001; Camargo et al. 2002; Hooper et al. 2002; Löf and Welander 2004; Stevenson and Smale 2005; Vieira and Scariot 2006; Doust et al 2008; Valkonen 2008; Motsinger et al. 2010; Grabau et al. 2011).

Control of grasses, forbs, and shrubs is required to ensure the proper environment (e.g. favorable light conditions, adequate soil moisture, available nutrients) for desirable seedling physiological response to result in better survival and growth (reviewed by Grossnickle 2000). A standard site preparation for direct seeding is to remove competitive vegetation by cutting, hoeing, use of herbicides, burning or mechanical removal (Schmidt 2008; Barnett 2014). In direct seeded studies where herbicides were applied to reduce plant competition establishment rates increased over control plots (Barron and Dalton 1996; Jinks et al. 2006; Ledgard et al. 2008; Balandier et al. 2009; Brooks et al. 2009; Willoughby and Jinks 2009). However, a strong response to herbicide application is not always reported (Wittwer 1991; Wang et al. 2011). Timing of herbicide application is critical because it can be damaging to emerging seedlings (Willoughby et al. 2003). The application of herbicides is an option, though caution needs to be applied to maximize benefits of this vegetation management treatment.

Not all existing vegetation at planting sites should be considered weeds, competing for energy, water, and nutrients of the direct seeded species (Ivetić and Devetaković 2016a). Under certain conditions the presence of vegetation cover promoted seedling emergence and survival in direct seeding programs (Ledgard 1976; Huebschmann and Wittwer 1992; Morris et al. 2000; Zimmerman et al. 2000; Hooper et al. 2002; Vieira and Scariot 2006; Bonilla-Moheno and Holl 2010; Davis et al. 2013; Avendaño-Yáñez et al. 2014, 2016; de Souza Gomes Guarino and Scariot 2014; Silva et al. 2015; Atondo-Bueno et al. 2016). In some instances seeds can attain higher germination under a grass canopy than on bare ground (de Souza Gomes Guarino and Scariot 2014), because grass cover protects from predators and improves microsite conditions. Exposed restoration sites can have a wide range of temperature and evaporative demand conditions, which can sometimes create planting stress (Grossnickle 2000). Compared to bare ground, seeds under grass canopy attain higher germination, but not the subsequent establishment of young seedlings (Pandey and Prakash 2014). Thus, one needs to consider whether vegetation cover is required to ameliorate extreme stressful site conditions that can affect seed germination or young seedlings growth.

Seed Predation

Seeds sown in the field are exposed to diseases, insects and rodents, which can result in low establishment rates. Predator activity is one of the major reasons for losses incurred in direct seeding programs (Caccia and Ballaré 1998; Cornett et al. 1998; Holl et al. 2000; Howlett and Davidson 2003; Hewitt and Kellman 2004; Pausas et al. 2004; Woods and Elliot 2004; Madsen and Löf 2005; Jinks et al. 2006; Vieira and Scariot 2006; Wennström et al. 2007; Erefur et al. 2008; Leverkus et al. 2013; de Souza Gomes Guarino and Scariot 2014; Helenius 2016). For example, seed predation can occur rapidly or gradually, but still over 80% of seed predation of *Pinus halepensis* occurred during the first six months after seeding (Figure 6). Jinks et al. (2012) suggested that species producing large nuts are more vulnerable to predation-loss and might require additional measures, such as treatment with repellents, to reduce the predation risk.

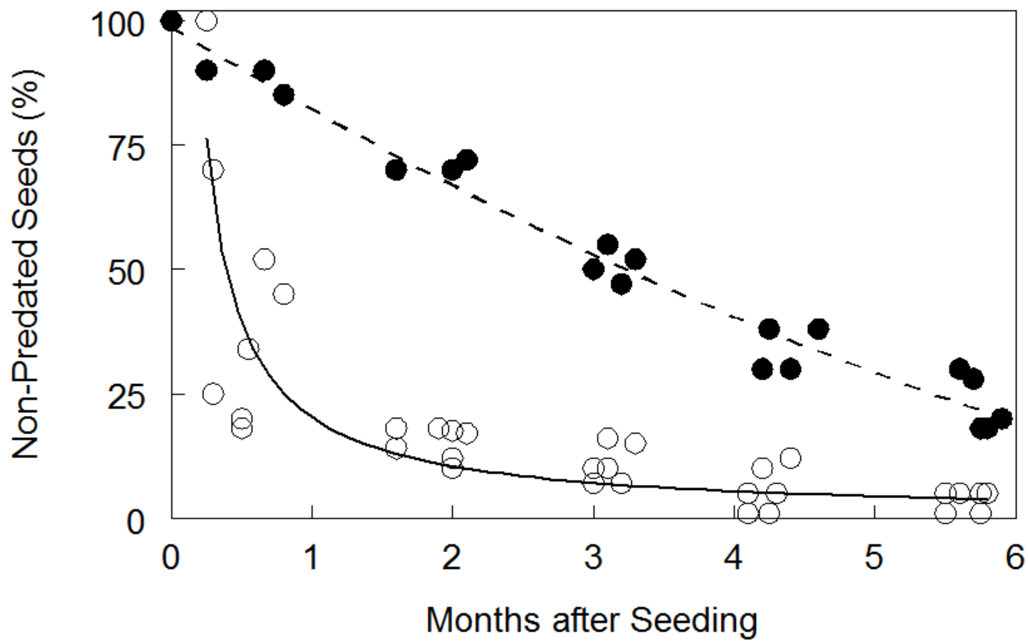

Figure 6. Percent seed predation (two response patterns over time) in an aerial seeding program with *Pinus halepensis* in a burned over area in Spain (adapted Pausas et al. 2004).

The uses of pesticides and rodenticides, as well as repellents or physical barriers are considered an option to prevent seed losses in direct seedling programs. For example, studies reported effective use of repellents to reduce rodent damage, with little effect on the seed germination (Barnett 1998, Nolte and Barnett 2000; Villalobos et al. 2017). However, repellents (Curtis et al. 1998) or cages (Caccia and Ballaré 1998) for *Pseudotsuga menziesii* seeds had limited success in preventing seed predation. In a study examining snap-trapping or raptor perches, neither resulted in increased direct seeded oak establishment (Birkedal et al 2009). This shows that these treatments cannot be considered a panacea to alleviate the seed predation problem.

Another suggested solution to reduce seed predation is the use of alternative foods to feed the rodent population and keep them from feeding on the tree seed crop. In one instance, the use of alternative food improved survival of conifer seed, via reduction of predation by rodents and birds (Sullivan and Sullivan 1984). Sullivan and

Sullivan (1984) felt that rodents preferred larger seeds of an alternative food source because they had greater food value. However, large field trials with both conifer and hardwood species found no benefits of a wheat cover crop to protect seedlings from browsing mammals (Willoughby et al. 2004).

Covering newly sown seeds is another option to reduce seed predation. A simple covering of soil on tropical (de Souza Gomes Guarino and Scariot 2014), temperate hardwood (Nilsson et al. 1996) and conifer (Nilson and Hjältén 2003) seeds with soil reduced losses from predation. Thus, covering seed may be an operational practice to reduce seed predation and increase the success rate of direct seeding programs.

4 Direct Seeding versus Seedling Comparison

The two main options available for the establishment of a forest stand on a restoration site are either direct seeding or planting of seedlings. Bareroot and container-grown seedlings are the two basic stocktypes used in forest restoration programs (reviewed by Grossnickle and El-Kassaby 2016). If one is to consider direct seeding, then one needs to understand how this practice performs in comparison to alternative means of establishing a forest stand (i.e. survival rate and growth).

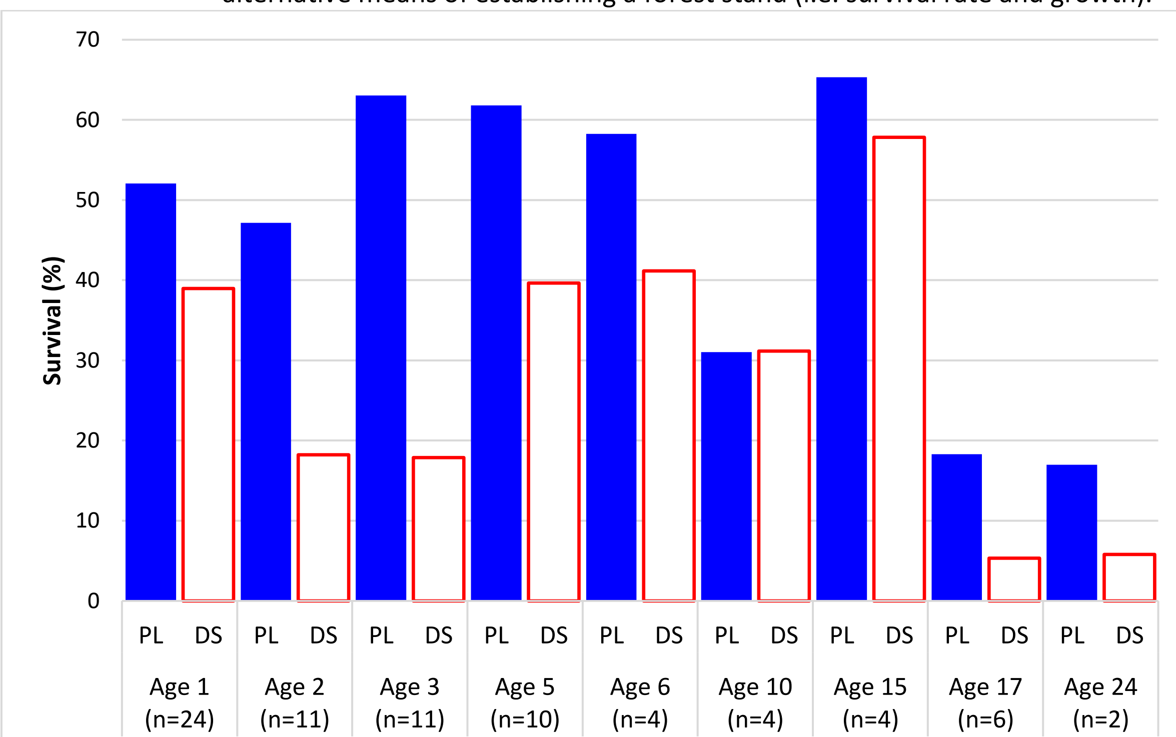

Figure 7. Survival comparison between planted seedlings (PL) and direct seeding (DS) for ages 1 to 24 after field planting for a range of broadleaved and conifer species (*Acacia saligna*; *Castanea dentata* x *C. mollissima*; *Eucalyptus gomphocephala*; *Picea abies*; *Pinus albicaulis*; *Pinus elliottii*; *Pinus flexilis*; *Pinus kesiya*; *Pinus sylvestris*; *Pinus taeda*; *Quecus ilex*; *Quercus nigra*; *Quecus nuttalli*; *Quercus pagoda*; *Quercus palustris*; *Quercus shumardii*; *Quercus suber*). All studies report both PL and DS field survival (only control treatments reported) (Noble 1985; Huebschmann and Wittwer 1992; Haywood and Barnett 1994; Ozalp et al. 1998; Williams and Craft 1999; Pausas et al. 2004; Varmola et al. 2004; Fields-Johnson et al. 2010; Motsinger et al. 2010; Smith et al. 2011; So 2011; Gonzales-Rodrigues et al. 2011; DeMastus 2013). Filled bars represent survival percentage of planted seedlings and empty bars represents survival percentage of direct seeded seedlings.

Trials comparing planted seedlings to direct seeding found that planted seedlings had a significantly higher rate establishment rate (i.e. up to 40-60% higher) (Wendel 1971; Campbell 1981; Noble 1985; James 1990; Huebschmann and Wittwer 1992; Ray and Brown 1995; DeLong et al. 1997; Schweitzer et al 1997; Williams and Craft 1998; Williams et al. 1999; Twedt and Wilson 2002; Löf et al. 2004; Dey et al. 2008; Motsinger et al. 2010; Cole et al. 2011; So 2011; Ammondt et al. 2013). These findings are corroborated in a recent review that found that on average planted seedlings had survival rates that were 44% higher (Pamela and Laurence 2015). In addition, higher survival rates continue well out into stand establishment, indicating that direct seeding will produce forest stands with a lower number of trees than planting seedlings (Figure 7), though in certain instances this practice has similar field survival as planted seedlings (Haywood and Barnett 1994 and Figure 7). In most cases direct seeding, compared to the planting of seedlings results in a lower rate of stand establishment.

Oak species typically have the greatest survival in direct seeding programs (Table 2) and perform well when compared to planted seedlings. For example, there was no significant difference in survival between direct seeded and planted seedlings of *Quercus ilex* when planted in harsh conditions (Oliet et al. 2015). Survival of direct seeded *Quercus* species was 34% compared to 53% for the recommended planted seedling stocktype in Mediterranean conditions (González-Rodríguez et al. 2011). In long term field trials (5-6 years) planting of oak seedlings resulted in 91% to 65% survival, while direct seeded seedlings had 56 to 53% survival (Zaczek et al. 1997; Valkonen 2008).

Seedlings established from direct seeding typically have slower growth compared with planted seedlings. In a four year field trial of *Pinus sylvestris* planted seedlings, initially greater in size, maintained a greater size and higher growth rate resulting in directed seeded seedlings being 50% smaller (Figure 8). Similarly, other studies showed planted seedlings had higher average height growth than direct seeded seedlings (Noble 1985) and direct seeded seedlings were 40% to 50% smaller than planted seedlings after four years in the field (Allen 1990; Stanturf and Kennedy 1996; Fleming et al. 2001; Parker et al. 2001; Pausas et al. 2004; Valkonen 2008). For *Quercus rubra*, only 12% of direct seeded seedlings exceeded the plantation mean height, based on container-grown planted seedlings, after three years (Zaczek et al. 1997). For temperate hardwood and conifer species growth differences between direct seeded and planted seedlings extended well into stand development with planted seedlings still greater in size five (Stanturf et al. 2009), ten (Smith et al. 1968; Densmore et al. 1999), 11 (Ackzell 1993), 15 (Haywood and Barnett 1994) and 17 years (Sharapov 1931, cited in Ivkov 1971) after stand establishment indicating that direct seeded seedlings grow slower in the field if they are smaller initially.

If direct-seeded seedlings are of a comparable size to planted seedlings after initial field establishment they can have the same or better growth rates. In a nine-year study comparing direct-seeded and planted seedlings of *Fagus sylvatica*, only the most dominant direct seeded seedling had comparable stem diameter or greater height growth than the overall population of 1+0 planted seedlings (Ammer and El Kateb 2007; Ammer and Mosandl 2007), whereas the overall population of 2+0 seedlings (i.e. larger at planting) had better growth (Ammer and Mosandl 2007). In another study, direct seeded *Quercus faciata* var. pagodaefolia, reached the same height and diameter of planted seedlings after five years at the field (Mullins et al. 1997). Stands of *Pinus concorta* established by direct seeding initially grew more slowly than planted stands, but actually grew faster once they reach a dominant height of 13–14 meters (Backlund and Bergsten 2012; Ahnlund Ulvcrona et al. 2013).

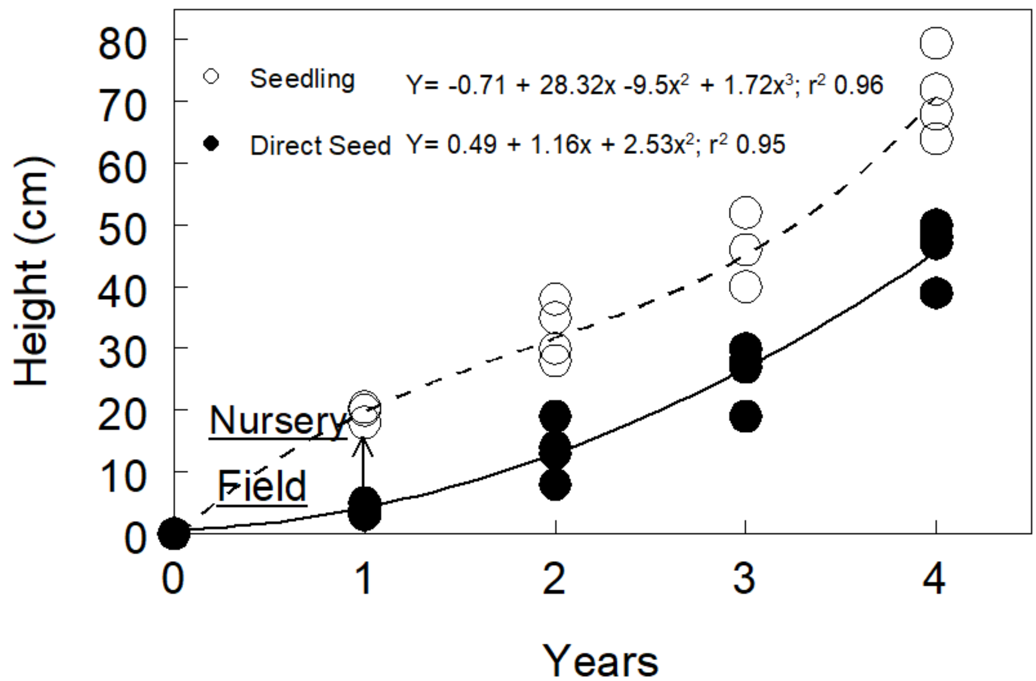

Figure 8. Shoot height development of seedlings and direct seeded *Pinus sylvestris* from multiple seed sources (adapted from Wennström et al. 2007). Height growth during the first year occurred either in the nursery or on the field site. Nursery grown seedlings were planted at the end of year one on the same site as direct seeded seedlings (arrow notes their field planting date).

Regeneration silvicultural practices, such as direct seeding or planting seedlings, provide a means for directing the course of the secondary forest successional process on restoration sites through the addition of desirable plant species (Grossnickle 2000), and the removal or suppression of undesirable plant species (Wagner and Zasada 1991). Site preparation or vegetation management practices can alleviate site resource competition, but this reduction in vegetative competition is ephemeral, meaning that seedlings need to be large enough to capture site resources and maintain growth that exceeds reinvasion of the site by plant competition. Studies have shown that planted seedlings with a larger shoot and root systems can have greater survival (Grossnickle 2012) and keep their size advantage over time (Grossnickle and MacDonald 2017) on sites with competing vegetation. To be a successful restoration option, direct seeding needs to establish seedlings that grow quickly and become large enough to capture site resources.

5 Operational Direct Seeding Practices

Since the 1970s, the use of direct seeding has declined to the point that it is now only a marginal component of forest restoration programs in most developed countries. For example, in Canada it is used in only in 3% of forest regeneration programs, with Ontario having the largest program at 13% of their reforestation program (Natural Resources Canada 2014). In the United States the last reported statistics (i.e. 1996), showed only 8,516 ha (less than 1% of all planting) were direct seeded (Moulton 1999). Currently, the amount of acreage direct seeded in the United States is so small that there are no available statistics on this practice (Hernandez, personal communication). In Europe, the few countries that report direct seeding information show a low (Sweden 5% - Ersson 2014); Serbia 15% (Ivetić, unpublished data)) to a moderate (Finland 22% (Finnish Statistical Yearbook of Forestry 2014)) amount of restoration acreage applying this practice. In northern and northwestern Russia, 43% of total artificial regeneration in 2002 was done by direct seeding (Leinonen et al. 2008). Application of direct seeding is said to be on a much larger scale in tropics, e.g. China and Vietnam (Schmidt 2008), and India (Pandey and Prakash 2014). From 1952 to 2008 a total of 30.7 million hectares was aerial seeded in China (Cao et al. 2011), with 136,400 ha in year 2012 (The National Forestry Bureau 2013).

5.1 Reasons for the Limited Use of Direct Seeding

Reasons for the limited use of direct seeding in developed countries can be attributed to a number of factors.

<u>*Required stocking of the site*</u>

Many operational reforestation programs require full site occupancy of desired tree species to be considered fully stocked with a defined criterion for number of saplings of a certain size within a given timeframe so the site is free-to-grow and no further regeneration silvicultural practices are required. Also, many forest industry programs have moved into plantation forestry where the even distribution of trees across the site is necessary to maximize stand yield (West 2014). In addition, nearly all levels of government now require proper restocking on any site that has been harvested. The following are examples from across developed countries.

- In North America there are recommended standards for the number of seedlings to be planted at a defined spacing to achieve full stocking of a harvested site (e.g. Oregon (Rose and Haase 2006) and in British Columbia (BC MoF Forest Regulations - https://www.for.gov.bc.ca/hfp/silviculture/stocking_stds.htm) or to maximize site productivity from the forest plantation (e.g. Southern US - Smith and Strub 1991) within a given timeframe.
- In southern Sweden there are minimal required planting densities of 2,000–4,000 seedlings per hectare for reforestation programs (Holmström et al. 2016).
- In Russia, minimum planting density depends on soil and stock type; 3,000 bareroot seedlings per ha on wet soils to 4,000 bareroot seedlings per ha on dry soils, with these number per hectare decreased to 2,000 (1,000 for container oak transplants) when transplants and containerized seedlings are used (Zhigunov et al. 2014).
- In Serbia, according to Forestry directorate rules the required minimum number of seedlings per hectare depends on species: for *Populus sp*. - 300, for *Prunus avium* and *Juglans regia* - 500, and 2,000 for transplanted seedlings of other species (Forestry Directorate 2016 funding regulations).

Intensive regeneration silvicultural practices are required to achieve these restocking standards. In many cases, there are restrictions to harvesting adjacent forest stands if the standards are not met. Direct seeding typically has low establishment rates (see Current Direct Seeding Research section) and slower growth rates (see Direct Seeding versus Seedling Comparison section) which results in 'patchiness' in stand establishment, limiting the ability to meet stocking standards within the required timeframe. Direct seeded sites may require an extra investment in planting seedlings to achieve adequate stocking (Kankaanhuhta and Saksa 2013). This difficulty for direct seeding to achieve stocking standards influences forest regeneration decisions towards planting seedlings.

Increased use of high quality seed

In many developed countries high-quality seed is used in reforestation programs. The following are some examples.

- In the Nordic region the use of improved seed from seed orchards has increased in recent years with 94–99% of *Picea abies* and *Pinus sylvestris* seedlings originating from seed orchards in Sweden, Finland and Norway (Rytter et al. 2016).
- In Great Britain 75%, and in Denmark 90% of *Picea stichensis* seed comes from seed orchards (Lee et al. 2013).
- In the Pacific Northwestern US, much of the *Peudotsuga menziesii* and *Tsuga heterophylla* seed, as well as nine "minor" conifer species used for reforestation on industrial and some public forest lands are produced in seed (Miller and DeBell 2013).
- In British Columbia Canada, select seed is used for 65% of the total provincial annual seeding of ~245 million seedlings (Forest Genetics Council of BC 2016).
- In the Southeastern US 100% of *Pinus taeda* and *Pinus elliottii* seed comes from seed orchards (1st through 3rd generation) to produce 850 million seedlings (South et al. 2016).

As tree improvement programs start to produce 1st to 3rd generation seed, the cost does not make it a viable option for direct seeding programs. For example, in British Columbia Canada the seed, for all tree species, used in the provincial seeding program typically has a germination capacity of >85% (Kolotelo personal communication). It becomes more logical to use this high-quality seed in seedling production programs where >90% of the seed is turned into plantable seedlings when grown in nursery programs under controlled environmental conditions (Landis et al. 1998) compared to the low conversion rates that typically occur in direct-seeding programs (see Current Direct Seeding Research section).

Improved seedling quality

For over 50 years, foresters have recognized quality seedlings are central to any successful forest restoration program (Wakeley 1954; Duryea 1985; Rose et al. 1990; Colombo and Nolan 1997; Grossnickle 2000; Riley et al. 2010). Since the mid-20th century an extensive amount of effort has gone into nursery cultural practices that improve seedling quality, which has translated into improved seedling survival (Grossnickle 2012) and growth (Grossnickle and MacDonald 2017) after planting in restoration programs around the world. The use of high quality seedlings can increase chances of successful seedling and forest stand establishment.

Time lag in seedling development

Seedlings produced from direct seeding compared to planted seedlings have slower development (i.e. reduced size) on the reforestation site (see Seedling Comparison section).

Operational Performance

Operational direct seeding programs show a range of results, from total failures to success (Table 3). In over one-half of these programs the final stocking rate did not meet management objectives. Reasons given for not meeting the program objective were similar to those described above (see Factors Affecting Conversion Rates section). For *Pinus massoniana* direct seeding was considered successful because stand development after age 21 was similar to natural regeneration (Xiao et al. 2015), while direct seeding of *Cedrus atlantica* was considered a success because it improved the site by establishing a forest stand (du Cross et al. 2004). Partial success occurred with *Pinus tabulaeformis* because direct seeding resulted in higher stand density, but lower growth rate, compared to seedling planting (Li et al. 2009). Ultimately one must define what is meant by reforestation success. If successful forest site restoration is defined as a fully stocked stand, then direct seeding needs to achieve at least an 80% restocking of the site to be a less expensive option than planting seedlings (Mitchell et al. 1991).

Table 3. Operational application of direct seeding in restoration programs and the reported program success result.

Program type	Species	Country	Application (1	Operational Result (2	Source
Reforestation sites	*Picea mariana*	Canada	SS	F	Fraser 1981
	Betula pendula and *B. pubescens*	Great Britain	GB	F	Willoughby et al. 2007
	Pinus tabulaeformis	China	AB	P	Li et al. 2009
	Pinus elliottii	USA	SS	S	Barnett 2011
	Various species	Brasil	GB	S	Campos Filho et al. 2014
	Pinus massoniana	China	AB	S	Xiao et al. 2015
Post-fire reforestation sites	Various species	USA	SS	F	Wahlenberg 1925
	Various species	New Zealand	GB	P	Ledgard and Davis 2004
	Enterolobium cyclocarpum	Mexico	AS	F	Garcia Cuevas et al. 2010
	Eucalyptus delegatensis	Australia	AB	S	Bassett et al. 2015
Afforestation Sites	*Pinus nigra* and *P. sylvestris*	Serbia	SS	S	Stamenković et al. 1994
	Various species	USA	SS	S	Stanturf et al. 1998
	Cedrus atlantica	France	GB	S	Du Cros et al. 2004
	Various species	Laos	GB and SS	P	Sovu et al. 2010
	Various species	China	AB	P	Cao et al. 2011

1) SS - Spot seeding, GB - Ground broadcast, AB - Aerial broadcast

2) S - success in most cases is defined by high or at least acceptable (by the forest authority) stocking rate, P – partial indicates some successful seedling establishment, F – failure is defined as low survival and establishment rate, and ultimately by low stocking rate; as defined in the citations.

5.2 Direct Seedling – Recommended Seeding Rates

Reforestation through direct seeding is applicable under conditions where seeds of woody plants can germinate and establish rapidly in response to vegetative competition (Schmidt 2008) and harsh environments (Chik 2004). The ability to stock the site through direct seeding is dictated by a number of factors defining program success.

Seedbed Receptivity

The term seedbed receptivity is defined as the number of ideal seeding microsites and the ability to deliver seed to those sites (Fleming et al. 2001). Seedbed receptivity can be expressed by the establishment ratio (i.e., number of established seedlings divided by the number of sown seeds), with this ratio dictated by species and site conditions (Groot 1994). The relationship between stocking percentage and seedbed receptivity is site limited because not all locations on a site are receptive. For example, in an assessment of 20 seedbed types, the establishment ratio ranged for 0.1% to 54%; with sheared flat surface of poorly decomposed peat being the most receptive site (Groot 1988).

Silvicultural practices are intended to improve site conditions and receptivity by reducing or rearranging slash, ameliorating adverse forest floor, soil, above- and below-ground vegetation structure, or modifying other site biotic factors (Daniel et al. 1979). Seedbed receptivity for direct seeding can be managed through silvicultural practices that expose more of the site to the optimum seed to seedling establishment pathway.

Seed Dispersion

How seed is spread across the restoration site is a critical step in ensure a fully stocked site (Groot 1988). Highest stocking rates are achieved when seed is uniformly spread across the site, though typical broadcast seeding practices usually results in a non-uniform distribution pattern (Figure 1B). This uneven seed distribution can be made up, in part, by ensuring there are enough receptive seedbed sites and increasing the seeding rate. The combination of seedbed receptivity and seed distribution dictates why furrow/line or spot seeding requires a lower seeding rate than broadcast seeding (Table 4) because these practices are more effective at distributing seeds to receptive seedbed sites.

Seeding Rate

The seeding rate is the most easily controlled variable in direct seeding systems. However, Groot (1988) warns that managers need to avoid merely increasing the seeding rate to try and achieve their stocking objective. For example, the amount of seed needed to achieve site stocking initially increases dramatically with seeding rate (up to 200,000 seeds to achieve 50%-60% stocking), with further amounts of seed resulting in a minimal increase in stocking levels (i.e. a diminishing benefit of additional amounts of seed), and never reaching full stocking (Figure 9). Seeding rate is a less important factor once the quantity sown is above a certain threshold (Farrelly et al. 2003) because limitations of seedbed receptivity cannot be overcome by just increasing the seeding rate.

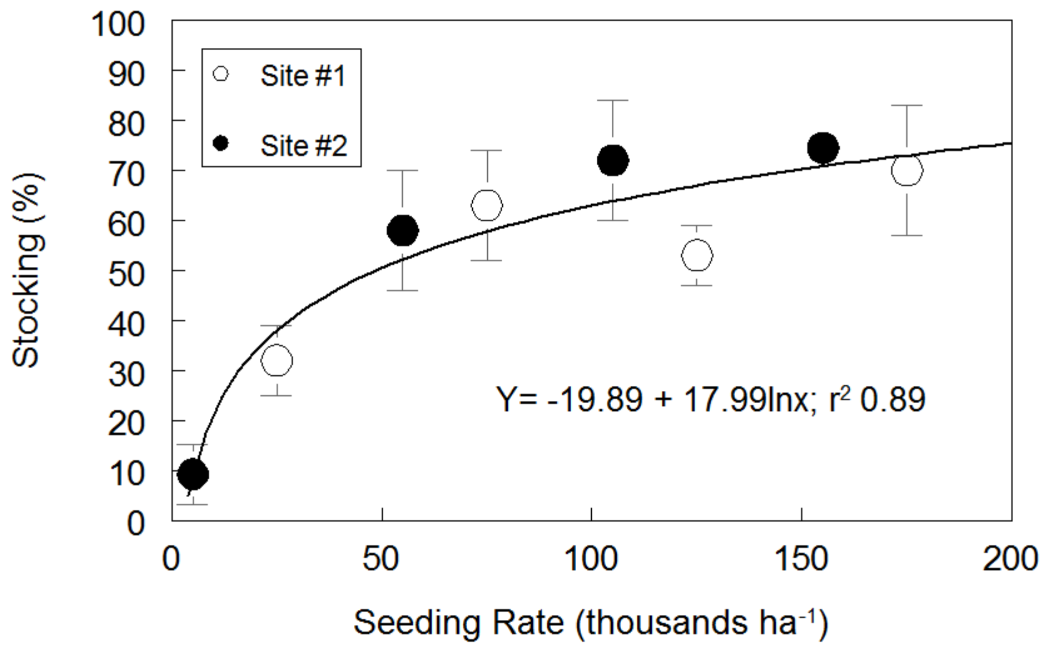

Figure 9. Stocking after five years (i.e. portion of quadrats stocked with at least one seedling) for *Picea mariana* across two boreal restoration sites with various broadcast seeding rates (adapted from Groot 1988).

Operational Seeding Rates

A number of developed countries have defined recommended direct seeding rates that are required to ensure a fully stocked stand in forest restoration programs across a wide range forest sites (Table 4). These seeding rates are high due to the low expected conversion rates (see Conversion Rates section). For example, *Pinus sylvestris* operational trials found the initial seedling establishment was normally between 10 and 20% even at rates of 50,000–60,000 seeds ha^{-1} (Helenius 2016). Trials conducted in Sweden found that to obtain a density of 5,000 stems ha^{-1} four years after seeding, 61,000 viable stand seeds ha^{-1} or 41,000 orchard seeds ha^{-1} were required if microsite preparation was not used (Wennström et al. 1999). Site scarification to the mineral soil and microsite preparation reduced seeding requirements to 32,000 stand seeds or 22,000 orchard seeds ha^{-1} (Wennström et al. 1999). Recommended seeding rates for hardwoods in the central United States is 7,500 ha^{-1} for drill seeding and 11,250 ha^{-1} for broadcast seeding (National Resources Conservation Services 2015). Interestingly, recommended direct seeding rates for oaks is quite low, with a seeding rate of 1,000 acorns ha^{-1} for restoring open oak woodlands in Mediterranean ecosystems (Sánchez-González et al. 2016) and ~2,000 to 4,000 ha^{-1} in marginal agricultural land in the lower Mississippi river alluvial valley (Stanturf et al 1998). However, direct seeding rates of oaks need to be 9 to 4.5 times greater for direct seeding through broadcast (6,500 ha^{-1}) or drill seeding (3,250 ha^{-1}) respectively, to achieve same the stand density of planted seedlings (730 ha^{-1}) (Lockhart et al. 2003). The lower seeding rate for oak species is probably dictated by having a relatively high establishment success rate (Table 2).

Table 4. Recommended operational direct seeding rates for a number of developed countries under various direct seeding practices.

	Seeding Rate (Seeds ha^{-1})		
Species	**Broadcast**	**Furrows/Line**	**Spot**
	Pacific Northwest of North America[1]		
Pseudotsuga menziesii	50,000 – 70,000	12,000 – 16,000	20.000
Pinus ponderosa	18,000	10,000	15.000
Larix occidentalis	90,000 – 140,000	16,000 – 24,000	21.000
	Western Boreal Forests of Canada[1]		
Interior spruce	100,000 – 200,000	20,000 – 24,000	21.000
Pinus contorta	70,000 – 80,000	16,000	15.000
	Eastern Boreal Forests of Canada[2]		
Pinus banksiana	25,000 – 100,000	15,000 – 30,000	15.000 – 30.000
Picea mariana	100,000 – 300,000		
	Southeastern Forests of the United States[3]		
Pinus taeda	30,000	5,300	9.000
Pinus palustris	37,000	7,200	10.750
Pinus elliottii	35,000	7,200	10.750
Pinus echinata	49,000	10,750	14.300
	United Kingdom[4]		
Fraxinus excelsior	200,000		
Quercus robur	100,000		
Betula pendula	200,000		
Acer pseudoplatanus	200,000		
Prunus avium	200,000		
	Finland[5]		
Pinus sylvestris		50,000 – 60,000	

[1] Mitchell et al. 1991; [2] Fleming et al. 2001; [3] Barnett 2014; [4] Willoughby et al 2004; [5] Helenius 2016

6 Potential Alternative Direct Seeding Practices

Improvements in the application of direct seeding for forest restoration programs requires better ways to create more effective seed dispersion, increase seedbed receptivity, minimize seed predation or create a more favorable microsite environment. In addition, seed enhancement technologies should be examined. These technologies apply seed coating to deliver materials such as nutrients, microbial inoculants and protection agents or hydration treatments to the seed that can enhance germination, emergence, and/or early seedling growth. Existing seed enhancement technologies used in agriculture and horticulture (reviewed by Halmer 2006) and other disturbed ecosystems (reviewed by Madsen et al. 2016) to enhance seed establishment success could provide useful options. The following are examples of proposed technology to increase direct seeding effectiveness for forest regeneration programs.

Seed Shelters

The function of seed shelters is twofold. First, seed shelters can modify the environment around the seed. Studies have found seed shelters can create a positive environment for the seed (i.e. decreases incoming solar radiation) (Kjelgren 1994; Bergez and Dupraz 1997; Bellot et al. 2002) (i.e. reduced vapor pressure deficit and wind speed) (Bergez and Dupraz 1997). Shelters can also have potential for negative effects on the growing environment (i.e. increase the temperature and vapor pressure deficit)

(Kjelgren 1994; Bellot et al. 2002) resulting in summertime conditions that can cause photoinhibition to seedling in shelters (Pemán et al. 2009).

Second, seed shelters can provide protection from predators (Caccia and Ballaré 1998; Fleming et al. 2001; Pausas et al.2004; Reque and Martin 2015). Direct seeding performance with seed shelters is reported in a number of studies. In one study seed shelters successfully promoted seed germination (1%–12% unprotected vs. 77%–84% protected) and seedling survival (1%–10% unprotected vs. 54%–74% protected) (Barton et al. 2015). Other studies have also reported increased seedling establishment with seed shelters (Caccia and Ballaré 1998; Densmore et al. 1999; Fleming et al. 2001; Pauses et al. 2004; Petursson and Sigurgeirsson 2004, Madsen and Löf 2005; Valkonen 2008; Castro et al. 2015; Repáč et al. 2017), though not under all field conditions (DeLong et al. 1997; Pausas et al. 2004). Seed shelters have also resulted in greater seedling growth (Pausas et al. 2004). In a literature review Ceccon et al. (2016) found that seed protection increased the probability of successful seed germination, though there was no benefit during seedling growth. Figure 10 (A, B and C) shows examples of seed shelters for direct seeding programs. Even if seed shelters increase success, however their use complicates the process of seeding and increases planting costs, thereby diminishing one of the biggest advantages of direct seeding compared to planting seedlings.

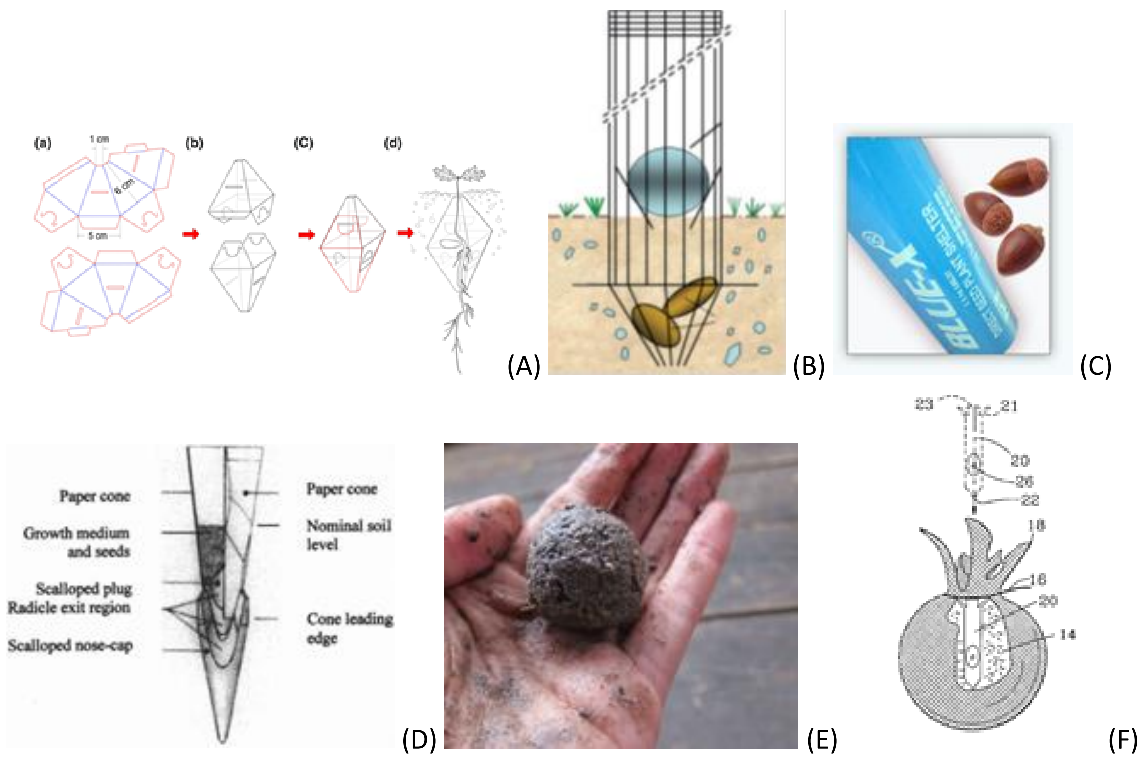

Figure 10. Examples of alternative practices for the application of direct seeding through the use of seed shelters: A) (Castro et al. 2015); B) Reque and Martin (2015); C) The BLUE-X® Direct Seed Plant Shelter (http://www.growtube.com/products/directseed/); or various delivery systems for aerial seeding: D) aerial dart seed delivery system (Wood 1984); E) a seed bomb (Ortolani et al. 2015); F) biodegradable seed pouch system (Fima 2003).

Hydro Seeding

An improved version of simply dropping the seed from the aircraft is hydro seeding or hydromulching. Hydro seeding was developed in the 1950s, and is a technique for distributing seeds in a slurry form combined with processed woodchip fibers and other optional enhancements, such as fertilizer and a tackifying agent (Schiechtl 1980; Becker 2001). Ideally hydro seeding creates a thin layer covering the seed; much like covering seed with topsoil, thereby improving seed germination (Schiechtl 1980). This technique is an effective seeding approach on steep and rocky slopes that are hard to seed or plant with seedlings. The main drawbacks of hydro seeding are the potential rapid deterioration of the cover layer under extreme weather conditions thereby exposing seed prior to germination (Schiechtl 1980) and the requirement for a large amount of water to create the slurry (i.e. low seed to cargo weight ratio) (Becker 2001). Hydro seeding also requires heavy equipment that is not easily moved through rough terrain. Hydro seeding is best used in programs where there is rapid access to a water source and a road system for ease of moving heavy equipment.

Alternative Aerial Direct Seeding Options

Aerial seeding of reforestation sites has been ongoing for decades. For example, in Canada aerial direct seeding was a main form of reforestation (i.e. fixed wing aircraft or helicopters) used in the 1960s and 1970s for ~50% of the total area seeded (Waldron 1973). Although aerial seeding is not a new concept, new aerial seeding application technologies have been developed for restoration programs as described below.

Seed Bundles

Seeds are put into packages where they are combined with various materials that are intended to benefit the seed after being distributed across the site. These seed bundles come in various forms.

- A seed-containing aerial dart (Figure 10D) serve as ground-penetrating containers for seeds (Wood 1984) (Figure 10D). Testing found that the best seed germination rates (45%) and survival rate (27% after 1 yr) occurred when seeds ended up being planted 1cm below the soil surface (Wood 2000).
- Aerial seed bombs are made from various substances as a way to deliver multiple seeds. In its most basic form these seed bombs are made with a clay shell (Figure 10E), which could also contain nutrients, chemicals to deter seed predators, symbiotic microbes and hydrogels (Ortolani et al. 2015). Experiments with seed bombs have been carried out with *Pinus sylvestris* seeds, *Quercus ilex*, *Quercus suber* and *Myrtus communis* (Ortolani et al. 2015). A similar version of this system is being used by the Thai government to reforest disturbed areas (https://youtu.be/IpN9-45XPrs). Trials have yet to define plant establishment success.
- Airborne seed pouches have the ability to partially penetrate the ground when delivered by an aerial system (Fima 2003). The pouch is a small biodegradable package containing seeds, along with soil and nutrients (Figure 10F). The pouch, spherical or conical in shape, includes a flared open end formed by constricting the skin to allow for a relatively slow descent when delivered by low flying aerial system. Additionally, there is an elongated vertical shaft to assist in orientation when dropped, to facilitate penetration into the ground and to release the package contents on impact.

- Pasta seed pillows are made up of Diatomaceous earth, bentonite clay, compost and worm castings. The nickel-sized pods contain native seeds, a special mix of plant nutrients and hydrogel. Controlled laboratory trials show improved performance over direct seeding with bare seed (Madsen et al. 2016).

Drones

Recent technological advances in unmanned aerial vehicles (or drones) and imaging systems raise the possibility of automating several of restoration tasks (Elliott 2016). Drones and new imaging devices have the potential to conduct site monitoring (i.e. assess site regeneration potential, plan interventions and assess progress), aerial seeding and vegetation management. There are a number of private companies using drones for addressing site management issues and to apply aerial seeding of restoration sites (BioCarbon Engineering - www.biocarbonengineering.com/; Droneseed - www.droneseed.co). Their intent is to map sites to define specific microsites that have the best chance for seed establishment, and then deliver seeds packets to these microsites, and follow-up with monitoring direct seeding success and applying precision spot spraying of herbicides for site vegetation management practices.

Conclusions

Direct seeding has the potential to address worldwide forest restoration programs. A major benefit of this option is that it can be done quickly, over large disturbed areas and at a relatively low cost. It also has the potential to create ecologically diverse forest stands that have a more natural root system form. However, direct seeding has low seedling establishment rates (i.e. typically around 20%) due to seeding practices, site conditions, seed predation and vegetation competition. In addition, seedlings established through direct seeding grow slower than planted seedlings, thus requiring additional silvicultural practices to ensure establishment of the desired forest stand. This is why the use of direct seeding as the sole means to achieve successful regeneration, without the inclusion of a seedling planting option, has been debated over the last century (i.e. from Toumey 1916 to Ceccon et al. 2016).

To be effective better practices are required to improve the success of direct seeding programs. It is important to recognize that successful forest restoration with direct seeding is more than just seed delivery to the site; it is a comprehensive process requiring many silvicultural factors to ensure program success. First, planning for the application of direct seeding, one needs to consider that seedbed receptivity and seed dispersion are just as important as seeding rate. Second a number of silvicultural practices need to be considered including: seed quality to ensure maximum conversion, timing of seeding and seeding practices for maximizing germination of the sown species, controlling seed predation, optimizing microsite environmental conditions and managing competitive vegetation. Ultimately, any determination of regeneration program success needs to consider all practices that are required to achieve a fully established forest stand. Even controlling these silvicultural practices does not guarantee a successful program, but by applying best practices one increases chances for improved success of direct seeding on forest restoration sites.

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