



Direct seeding is more cost effective than container stock across ten woody species in California

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ABSTRACT

The planting of native woody plants is a cornerstone of many habitat restoration projects. Current techniques for revegetating disturbed or reclaimed plant communities often consist primarily of planting trees and shrubs from container stock, which can be costly to buy or produce, time-consuming to plant (an additional cost), and logistically difficult for large-scale restoration projects. We tested whether direct seeding woody species was more cost effective than planting container stock. During fall 2004, we planted 3 sites encompassing the ecotone of foothill riparian and woodland habitats in northern California with 10 native species of woody plants, both as container stock and direct seed. Data on survival were collected over a 2-y period. Across species, the planting success of direct-seeded plants, but not container plants, increased significantly with increasing mean seed size. Although seeds generally had lower individual planting success than did container stock, this was always offset by the higher costs of purchasing and planting container stock. Direct seeding was up to 29 times more cost effective than planting container stock when considering base costs (not including fixed costs of tubes, irrigation, and herbicide). Including these additional costs reduced the cost advantage, but direct seeding remained more cost effective per surviving plant across all species, and especially so for large-seeded species.

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KEY WORDS

planting costs, restoration, native plants, seed size

NOMENCLATURE

Hickman (1993)

Establishment of native woody plant species is a cornerstone of many ecological restoration projects worldwide (Maunder 1992). Revegetating disturbed or reclaimed areas often includes planting trees and shrubs from container stock, usually plants initially grown in a nursery (Walmsley and Davy 1997; Matthes and others 2003; Burkett and others 2005; Ruiz-Jaen and Aide 2005; Alvarado-Sosa and others 2007), in part because most restoration projects seek to optimize the survival of individual plantings (Falk and others 2006). Container stock of woody species generally has higher survival than seeds (but see review by Young and Evans 2001) and has been used more widely than direct seeding (Ruiz-Jaen and Aide 2005). Planting container stock bypasses the most vulnerable life stages: pre-germination losses, germination, and initial establishment (Grubb 1977). Many current restoration protocols, however, have not been evaluated for their efficacy or cost efficiency (Clewell and Rieger 1997; but see Walmsley and Davy 1997; Matthes and others 2003 for comparisons of different container stocktypes). In particular, the cost-effectiveness of direct seeding and container stock has not been compared. The greater cost of purchasing and planting container stock may exceed any survivorship advantage over direct seeding.

Quantifying the relative cost-effectiveness of containers with direct seeding is necessary because planting trees and shrubs from container stock can be prohibitively costly, time-consuming, and logistically difficult for large-scale restoration projects, especially those implemented by private landowners (Benayas and Camacho-Cruz 2004). Because of these difficulties, projects are often limited in scale (Stanturf and others 2001). If planting costs are reduced, restoration and conservation efforts could be applied on a broader scale (Clewell and Rieger 1997).

The difficulty of establishing trees from nursery-grown plants is especially evident in harsh or remote rangeland sites where irrigation and adequate site preparation (digging or augering holes) are more problematic. Moreover, the logistical difficulty of ensuring that container stock is planted correctly by hired crews or volunteers in remote or large-scale projects can lead to low survival rates. Rooting problems sometimes associated with container stock may limit their efficacy in restoration settings, and in some cases these problems have led to lower absolute survivorship or growth in container stock than from direct seeding (Halter and others 1993; McCreary 1995, 1996; Welch 1997; Young and Evans 2005; see review in Young and Evans 2001). Even when container stock has greater survival than direct seeding, direct seeding may be a more cost-effective way to implement large-scale restoration projects because of far lower costs per plant. Direct seeding was as effective as container stock in the establishment of valley oak (*Quercus lobata* Née [Fagaceae]) (Young and Evans 2001), but we lack 1) a comparison across multiple species and 2) an analysis of cost-effectiveness of the 2 approaches. Planting suc-

cess of direct-seeding grass species may increase with seed size (Lulow and others 2007), and this may be true in woody species also (Camargo and others 2002; Hooper and others 2002; Lockhart and others 2003; Khurana and Singh 2004; Doust and others 2006), affecting the cost-effectiveness of the 2 planting methods. To test the cost-effectiveness of direct seeding with container stock, we examined 10 native species in Yolo and Butte counties in California.

HYPOTHESES

- H1. Container stock will have greater survivorship than directly seeded plants.
- H2. Across species, the planting success of direct-seeded plants, but not container stock, will be positively correlated with seed size.
- H3. The higher mortality rates in direct-seeded plants will be more than offset by the lower costs in acquiring and planting seeds; the cost per surviving plant will be lower for direct seeding than for container stock.
- H4. The cost-effectiveness of direct seeding compared with planting container stock will increase with increasing seed size.

METHODS

Study Sites

All of the study sites are located in the northern Central Valley and foothills of California. The climate is strongly Mediterranean, with little or no rainfall during the summer months and mean rainfalls ranging from 635 to 1016 mm (25 to 40 in) per year.

Bobcat Ranch

Bobcat Ranch is a 2800-ha (7000-ac) cattle ranch outside of Winters, California (lat 38.6°N, long 122.0°W; elevation 54 m [180 ft]). The soil is a Rincon silty clay loam (Mollic Haploxeralfs) (California Soil Resource Lab 2010). The ranch was once dry-land farmed for wheat but has been grazed with cattle for at least the past 30 y. The vegetation ranges from blue oak (*Quercus douglasii* A. DC [Fagaceae]) savanna and woodland into chaparral in the higher elevations (Figures 1 and 2). The restoration goals for this site included extending the riparian corridor out from the creek into an oak savanna complex and establishing an understory of native grasses.

Stone Ranch

Stone Ranch is a 3000-ha (7500-ac) cattle ranch approximately 32 km (20 mi) north of Winters, California (lat 38.6°N, long 122.1°W; elevation 55 m [185 ft]). The soil is a

Tehama loam (Typic Haploxeralfs) (California Soil Resource Lab 2010). The vegetation ranges from blue oak savanna and woodland into chaparral at the higher elevations. The restoration goals for this site included revegetating a pond adjacent to the riparian corridor with native woody species and establishing an understory of native grasses.

Farview Ranch

Far View Ranch is a 4000-ha (10,000-ac) cattle ranch 4.8 km (3 mi) west of Bangor, California (lat 39.4°N, long 121.4°W; elevation 60 m [200 ft]). The soil is a Dunstone-Loafercreek Complex (Ultic Haploxeralfs) (California Soil Resource Lab 2010). For the past 40 y the ranch has been maintained as a cattle ranch. The vegetation is consistent with blue/valley oak savanna and woodland. The goals of restoration were to establish native woody species along the creek and to bolster the relic native grasslands.

Study Species

The 10 study species (Table 1) were chosen because of their common use in local restoration projects in northern California and because of their presence at reference sites. These species represented a range in mean reported seed size of more than 6 orders of magnitude (millionfold).

Planting

In the fall of 2004 at each site, container plants and seeds were planted in riparian/woodland corridors fenced to exclude cattle. Seeds for the direct seed treatment were collected within an 8 km (5 mi) radius of the site, treated, and direct seeded by hand at densities outlined in Table 2. Seed densities were based on observed germination and mortality rates in a nursery setting. Seeds were planted by breaking up the ground in a 7.5 to 15 cm (6 to 10 in) diameter circle. All seeds were pressed into this circle so that the top of the seeds were level with the parent soil. Seeds were then covered with an amount of soil approximately equal to 2 times their diameter. The exception for this was California buckeye (*Aesculus californica* (Spach) Nutt. [Hippocastanaceae]) which, because of its extremely large seed size, was covered with approximately 1.3 to 2.5 cm (0.5 to 1 in) of soil. Container plants were grown in D-40 Deepots™ (6.35 cm [2.5 in] diameter, 25 cm [10 in] depth, 656 ml [40 in³] volume, and a density of 174.4/m² [16.2/ft²]). Container plants are generally grown for one year prior to outplanting, although there may have been variation. Container plants and seeds were planted within gradients of proximity to the stream appropriate for each species. We installed 15 replicates of both seeds and containers for each species. Plantings were protected with a plastic tube (Tubex™, Aberdare, Mid Glamorgan; General phone +44 (0)1685 883 833, Sales phone +44 (0)1685 888 000). Weeds within a meter (3 ft)



Figure 1. View of study site at the Audubon Bobcat Ranch. Photo by



Figure 2. Replicates at the Audubon Bobcat Ranch study site. Photo by

TABLE 1

Information on the 10 species used in the experiment.

Latin Name	Common name	Growth form	Height (m)	Elevation (m)	Habitat	Seeds per gram
<i>Aesculus californica</i>	California buckeye	Tree	5–12	< 1700	Dry slopes, canyons, borders of streams	0.028
<i>Alnus rhombifolia</i>	White alder	Tree	35	100–2400	Along permanent streams	1478
<i>Baccharis pilularis</i>	Coyote brush	Shrub	3	< 750	Coastal bluffs, oak woodland	17,857
<i>Ceanothus cuneatus</i>	Buckbrush	Shrub	3	< 1800	Dry fans, slopes, ridges	116
<i>Cercis occidentalis</i>	Redbud	Shrub	2–8	100–1500	Dry slopes, canyons, streambanks, chaparral, foothill woodlands	100
<i>Cercocarpus betuloides</i>	Mountain mahogany	Shrub	2–8	< 2500	Chaparral, pine/oak woodland, conifer forest	27 ^Z
<i>Fraxinus latifolia</i>	Oregon ash	Tree	25	< 1700	Canyons, streambanks, woodland	18 ^Z
<i>Heteromeles arbutifolia</i>	Toyon	Shrub	5	< 1300	Chaparral, oak woodland, mixed-evergreen forest	52
<i>Pinus sabiniana</i>	Ghost pine	Tree	38+	150–1500	Foothill woodland, oak woodland, and chaparral,	1.3
<i>Sambucus mexicana</i>	Mexican elderberry	Shrub	2–8	< 3000	Streambanks, open places in forest	455 ^Z

Note: Nomenclature and other information from Hickman (1993). Seed size from Young and Young (1992).

^Z Seed size information based on species of the same genera with seed dimensions similar to the listed species.

Conversions: m = 3.3 ft; seeds per gram x 453.6 = seeds per pound.

TABLE 2

List of study species sorted by site and pre-planting seed treatments.

Species	Site	Seed treatment	Stratification	Planted as germinants	Seeds pertube (number)
<i>A. californica</i>	Bobcat 1, FVR	None	None	No	1–2
<i>A. rhombifolia</i>	FVR	Removed from strobili	None	No	~20
<i>B. pilularis</i>	Stone	None	N/A	Yes	2
<i>B. pilularis</i>	Bobcat 1&2, FVR	None	N/A	No	~10
<i>C. cuneatus</i>	Stone	Seeds boiled for 2 min and allowed to soak 24 h	3 mo	Yes	2
<i>C. cuneatus</i>	Bobcat 1, Stone	Seeds boiled for 2 min and allowed to soak 24 h	3 mo	Yes	2
<i>C. cuneatus</i>	Bobcat 2, FVR	Seeds boiled for 2 min and allowed to soak 24 h	None	No	6
<i>C. betuloides</i>	Bobcat 1	None	3 mo	Yes/No	2–5
<i>C. betuloides</i>	Bobcat 2	None	None	No	5
<i>C. betuloides</i>	Stone	None	3 mo	Yes	2
<i>F. latifolia</i>	FVR	None	None	No	6
<i>H. arbutifolia</i>	Bobcat 1&2, FVR	Scarified in a blender with blades taped	None	No	~10
<i>H. arbutifolia</i>	Stone	Scarified in a blender with blades taped	3 mo	Yes	2
<i>P. sabiniana</i>	Bobcat 1, Stone	Seeds cracked, soaked in water 12 h	3 mo	Yes	2
<i>P. sabiniana</i>	FVR	Seeds cracked, soaked in water 12 h	None	No	3
<i>S. mexicana</i>	Bobcat 1	Scarified in a blender	3 mo	No	~20
<i>S. mexicana</i>	Stone	Scarified in a blender	3 mo	Yes	2
<i>S. mexicana</i>	FVR	Scarified in a blender	N/A	No	~20

Note: Scarification was achieved by blending seeds for 30 sec or until seed was exposed beneath any fruit. Stratification was at 1 °C (34 °F) in bags of moist vermiculite.

diameter area around the tubes were controlled with glyphosate herbicide applied after planting and after the first flush of weeds. Drip irrigation systems were installed with emitters that delivered 3.7 l/h (1 gal/h) at each plant or direct-seed location. Irrigation systems were operated once every 2 wk for 5 to 8 h. Irrigation was used for 2 summers except at the Stone site, which was irrigated only the first year. Plants were numbered and tagged for monitoring. Every 3 mo survival data were collected. Each tube with a direct seed treatment was considered a single unit of replication regardless of number of seeds planted, and “planting success” was scored when at least one surviving individual was observed. We thought this value would be the most relevant to practitioners. Tubes with multiple seeds were not thinned. Seven species were planted at each site (see Table 2). Site-specific details were as follows.

Bobcat Ranch

Container plants and seeds of 7 species of foothill riparian/woodland species were planted as paired replicates (15 pairs per species) into pre-augered holes during November 2004. Container stock was purchased from a local nursery and the provenance of all species was within the Sacramento Valley. The intra-pair spacing was 1 m (3 ft) and the inter-pair spacing was 2 m (6 ft). Seeds of 4 species planted during fall 2004 experienced almost complete failure: *Baccharis pilularis* DC. (Asteraceae), *Cercocarpus betuloides* Torrey & A. Gray (Rosaceae), *Cercis occidentalis* Torrey (Fagaceae), and *Heteromeles arbutifolia* (Lindley) Roemer (Rosaceae). These species were replanted in November 2005 and subsequent success suggests that the poor survival during 2004 was due to artifacts of collection or planting technique. Regardless, however, results from both plantings were averaged and used in the analyses.

Stone Ranch

Container stock and seeds of 7 species were planted at a 2 to 4 m (6 to 12 ft) spacing across the site in January 2005. Container stock was purchased through a local nursery and the provenance was somewhere within the Sacramento Valley. The 15 replicates of each treatment were not paired but were replicated 15 times throughout the site. All direct-seeded plants were planted as pre-germinated seedlings and holes were not pre-augered. The Stone Ranch planting included *Ceanothus cuneatus* (Hook.) Nutt. (Rhamnaceae), which was not planted at the other sites.

Far View Ranch

Seeds and container stock were planted at a 2 to 4 m (6 to 12 ft) spacing across the site. Container stock was grown in an on-site nursery with seeds collected within a 8 km (5 mi) radius of the site. Three species were planted only as seeds: *Aesculus californica*, *Cercis occidentalis* (Figure 3), and *Alnus rhombifolia* Nutt. [Betulaceae]. Far View included 2 species that were not present at the other sites:



Figure 3. Redbud (*Cercis occidentalis*) seedling in tree shelter. Photo by

Oregon ash (*Fraxinus latifolia* Benth. [Oleaceae]) and white alder (*Alnus rhombifolia* Nutt. [Betulaceae]).

Statistics

We had *a priori* expectations that 1) species would differ in their overall planting success; 2) container stock and direct seeding would tend to differ in planting success; and 3) this difference would vary among species (species x treatment interaction). Although overall differences in planting success may occur across sites, we anticipated that the relationship between treatment and species would not differ among sites (nonsignificant 3-way interaction). All species were not present at all sites, and therefore a complete logistic analysis of planting success was not possible. We did, however, carry out a 3-way logistic fit analysis of planting success of container and direct seeding across the 3 species that were present at all 3 sites, and a similar analysis across the 6 species that were present at 2 sites (Stone and Bobcat), using JMP statistical software (SAS, Cary, North Carolina). The analyses revealed no significant species x treatment x site effects ($P = 0.40$ and 0.66 , respectively). Wahlsten (1991) pointed out that there is relatively low power to detect interactions in multi-way ANOVAs and suggested raising the alpha level for significance. The P values we found for the 3-way interaction, however, exceed even generous alpha levels. We therefore carried out similar 2-way logistic fit analyses on these 2 data sets, omitting site as a factor.

The relationship (across species) between mean seed size (ln-transformed) and planting success of directly seeded sites and container stock was compared with regression analysis. The cost-effectiveness of direct seeding versus container stock was tested against the null hypothesis of identical cost (relative cost = 1) for the 3 amendment scenarios.

Cost Calculations

For each species at each site, we calculated the cost-effectiveness of seeds and container stock by multiplying the mean planting success for that class by the cost of procuring, preparing, and planting it. We assumed a base labor cost of US\$ 10/h for all tasks. Our first set of calculations did not consider costs that seeds and containers shared in this experiment: tree shelters, irrigation, herbicide applications, staking, and set up/clean up. The 2 most costly interventions were included in the second set of analyses.

Seed cost

Initial seed costs consider only labor for collecting and storage. Access to a given seed source is often free (roadsides and other public access or willing private landowners). For each species and each cost category, we made high- and low-cost calculations based on personal experience, field trials, and interviews with restoration professionals. These cost calculations represent the range of costs within each cost category in order to account for the most variability. We then used the mean of these two for cost-effectiveness calculations. Planting time for seeds includes only the time needed to break up the ground in a 7.5 to 15 cm (6 to 10 in) diameter circle, place seeds, and cover them with soil.

Container cost

Container stock was obtained from 3 Sacramento area native plant nurseries: Cornflower Farms, Hartland Nursery, Floral Native Nursery. Mean costs for each cost category were calculated as described above.

All containers were D-40s (see above). Although cost-savings with smaller container size may be possible, the corresponding planting success of smaller container plants is unknown and might be lower. Additional space/storage costs must be factored in for containers. Container plants are much heavier and take up far more space than seeds. Base labor costs included only the time that it would take at a given planting site to dig a hole deep enough for the plug, remove the plant from the container and place it in the hole, and fill and pack soil around the plant. This time was based on personal field trials and conversations with restoration professionals.

The costs of planting amendments (irrigation and tubing) for seeds and container stock were calculated from the cost of the experiment.

RESULTS

In the full 3-way analysis of planting success across 3 species at 3 sites, planting treatment, site, and the species x site interaction were significant (Table 3A). This was due to greater overall planting success at the Bobcat site for *Sambucus mex-*

icana C. Presl (Caprifoliaceae) and *Pinus sabiniana* Douglas (Pinaceae) (Figures 4 and 5) but not for *Heteromeles arbutifolia* (Figure 6). In the broader analysis of 6 species across Bobcat and Stone, planting treatment and site were nonsignificant (Table 3A). In both analyses, site had no significant effect on the relationship between species and planting treatment (nonsignificant 3-way interactions). When analyzed without site effects (Table 3B), the container plantings had overall greater success than did direct seeding (Table 4), but this difference varied across species (significant species x treatment effects).

Planting success of direct-seeded stock ranged from 6 to 89% and was significantly positively related to mean seed size across species ($r^2 = 0.59$, d.f. = 9, $P < 0.01$; Figure 7A). Because direct planting success values are for entire tubes, regardless of whether more than one seed was planted, the per seed survivorship was even lower (although not quantified) for the smaller-seeded species, which had more seeds planted per tube (see Table 2). Therefore, our correlation analysis was conservative with respect to the positive relationship between seed size and per-seed survivorship.

Container survivorship ranged from 12 to 93% and was not significantly related to seed size across species ($r^2 = < 0.01$, d.f. = 8, $P > 0.99$) (Figure 7A). A lack of significance could be due to a lack of statistical power, but the correlation coefficient was very low (nowhere near significance), and even without the smallest-seeded outlier, we found no significant relationship. This combination of relationships resulted in a pattern of relative planting success advantage of container stock over direct seed declining with increasing seed size, but this was not statistically significant ($r^2 = 0.29$, d.f. = 8, $P = 0.17$) (Figure 7B).

For all 10 species, the higher mortality of seeds was offset by the higher initial costs of stock plus the added planting (labor) costs (Table 5). The relative base cost of establishing a plant by means of container stock was 1.55 to 29 times more costly per survivor than by way of direct seeding ($P < 0.005$; Figure 8). This base cost does not include the (high) per-plant cost of tubes, irrigation, or herbicide. However, because the base cost ratio of every species is above 1.00, the relative cost-effectiveness will always remain > 1.00 , regardless of these fixed costs. Adding the fixed cost of tubes and irrigation reduces the seed advantage considerably, with container stock costing 1.23 to 6.56 times more per survivor than direct seeding (Table 6). Although the cost advantage of seeds declines with increasingly costly amendments, at all levels, direct seeding was significantly more cost effective than container stock (all $P < 0.005$, Figure 8). For most species, direct seeding is still more than twice as cost effective as containers. Although we noted a tendency for the cost advantage of direct seeding over container stock to increase with increasing seed size, this was not statistically significant (all $P > 0.23$).

TABLE 3A

Results of 3-way logistic analyses (Wald Chi-square) of the effects of species, site, and planting type (container plants versus direct seeding) on planting success.

Source	3 SPECIES 3 SITES			6 SPECIES 2 SITES		
	df	X ²	P	df	X ²	P
Species	2	4.66	0.10	5	8.32	0.14
Site	2	21.32	< 0.001	1	0.04	0.84
Container/Seed	1	6.53	0.01	1	0.26	0.60
Species x Site	4	16.36	0.003	5	3.70	0.59
Species x Container/Seed	2	3.79	0.15	5	5.02	0.41
Site x Container/Seed	2	3.79	0.15	1	0.05	0.82
Species x Site x Container/Seed	4	4.04	0.40	5	3.26	0.66

TABLE 3B

Results of 2-way logistic (Wald Chi-square) of the effects of species and planting type (container plants versus direct seeding) on planting success.

TABLE 3B

Source	3 SPECIES 3 SITES			6 SPECIES 2 SITES		
	df	X ²	P	df	X ²	P
Species	2	3.84	0.15	5	8.91	0.11
Container/Seed	1	3.94	0.05	1	27.1	< 0.001
Species x Container/Seed	2	6.26	0.05	5	18.3	0.003

TABLE 4

Planting success (proportion of planting sites with survivors) of plants from containers (C) and direct seeding (DS) for the 6 species planted in at least 2 sites.

Site	Bobcat		Stone		Far View Ranch	
	C	DS	C	DS	C	DS
<i>B. pilularis</i>	0.60 (15) ^Z	0.23 (30)	1.00 (15)	0.20 (15)	—	—
<i>C. betuloides</i>	0.67 (15)	0.30 (30)	0.27 (15)	0.21 (14)	—	—
<i>C. occidentalis</i>	0.80 (15)	0.33 (30)	0.53 (15)	0.00 (15)	—	—
<i>H. arbutifolia</i>	0.73 (15)	0.33 (30)	0.27 (15)	0.47 (15)	0.80 (5)	0.40 (15)
<i>P. sabiniana</i>	0.93 (15)	0.67 (15)	0.47 (15)	0.21 (14)	0.60 (15)	0.27 (15)
<i>S. mexicana</i>	0.67 (15)	0.73 (15)	0.40 (15)	0.47 (15)	0.12 (25)	0.07 (15)

^Z Sample size in parentheses.

DISCUSSION

The planting success of directly seeded plants was positively correlated with seed size (see Figure 7A). A similar pattern for restoration plantings has been shown for grasses at a northern California restoration site (Lulow and others 2007) and for tropical woody species (Camargo and others 2002; Hooper and others 2002; Khurana and Singh 2004; Doust and others 2006), but this appears to be the first test for woody species in a temperate restoration setting. This effect is likely due to the greater reserves in large seeds, and their greater ability to quickly establish larger root systems (see Sanchez-Gomez and others 2006 and references therein). Baker (1972) observed that species in drier habitats on average had larger seeds, which could be interpreted as a hedge against water stress. In our study, we found it interesting that even irrigated plants showed a positive relationship between seed size and planting success.

With few exceptions, the planting success of container plants was higher than for seeds (see Table 4). Although the literature contains exceptions to this trend (reviewed in Young and Evans 2001), this appears to be one of the main reasons why the use of container stock has been a widely used practice. Indeed, direct seeding can sometimes lead to complete failure (Matthes and others 2003). The lack of a relationship between seed size and planting success of container stock suggests that seed size advantages are expressed only very early in life, at least under these conditions (see Figure 7B).

Container stock was, however, less cost effective than direct seed, often by a considerable amount, because the greater cost of acquiring and planting container stock more than offsets its survival advantage (see Figure 8). The relative base cost-effectiveness of seeds over containers ranged from 1.6 to 29. Because this ratio was always greater than unity, no additional costs applied equally to both seeds and containers could make seeds less cost effective than containers. However, including costly interventions, such as irrigation and tubes, reduced the cost advantage of seeds because the (different) base costs become a smaller proportion of the total costs. Nonetheless, across both high- and low-cost calculations for most species, direct seeding was still more than twice as cost effective as containers. In large-scale projects even this small difference could result in notable cost savings. An additional potential advantage of direct seeding over planting container stock is that direct seeding may avoid forms of genetic selection that can occur in greenhouse production and some of the issues that arise with tap-rooted species grown in containers (Young and Evans 2001).

Our analysis suggests that target densities could still be reached by over-planting with direct-seeded individuals, especially for smaller-seeded species. Such compensatory planting, however, comes with the additional costs of tubes, irrigation, maintenance, and all other treatments, unless each planting site is over-planted and later thinned back to a single individual.



Figure 4. Foothill pine (*Pinus sabiniana*) seedling. Photo by



Figure 5. Foothill pine (*Pinus sabiniana*) seedling with tree shelter and irrigation. Photo by

TABLE 5

Base cost of seeds and container stock: the cost of the seeds or container stock, and the cost of getting them to the site and putting them in the soil.

SPECIES	SEEDS																
	Collection Seeds/h	Treatment Seeds/h	\$/seed	Seeds/site	Sites/h	Planting \$/site	Total \$/site	Survival/site	\$/survivor	Stock cost	Container/h	Cost/site	Cost ratio	Survival/site	\$/survival	Survival ratio	Relative base cost (container/seed)
<i>A. californica</i>	200	300	0.083	2	60	0.167	0.250	0.88	0.285	3.5	13.5	4.241	14.89	0.6	7.068	0.68	24.82
<i>A. rhombifolia</i>	4500	6000	0.004	20	60	0.167	0.171	0.06	2.729	3.5	13.5	4.241	1.55	1.0	4.241	16.00	1.55
<i>B. pilularis</i>	7500	10000	0.002	20	60	0.167	0.169	0.22	0.78	3.5	13.5	4.241	5.44	0.8	5.301	3.69	6.80
<i>B. pilularis</i> ^z	7500	10000	0.020	20	60	0.167	0.169	0.29	0.585	3.5	13.5	4.241	7.25	0.8	5.301	2.77	9.06
<i>C. betuloides</i>	200	300	0.083	5	60	0.167	0.250	0.27	0.916	3.5	13.5	4.241	4.63	0.47	9.087	1.71	9.92
<i>C. cuneatus</i>	750	1000	0.023	5	60	0.167	0.190	0.38	0.507	3.5	13.5	4.241	8.37	1.0	4.241	2.67	8.37
<i>C. occidentalis</i>	800	1200	0.021	5	60	0.167	0.188	0.22	0.852	3.5	13.5	4.241	4.98	0.67	6.361	3.03	7.46
<i>F. latifolia</i>	400	600	0.042	6	60	0.167	0.208	0.27	0.78	3.5	13.5	4.241	5.43	0.93	4.544	3.50	5.82
<i>H. arbutifolia</i>	600	1000	0.027	20	60	0.167	0.193	0.38	0.505	3.5	13.5	4.241	8.40	0.54	7.811	1.42	15.47
<i>P. sabiniana</i>	200	500	0.070	3	60	0.167	0.237	0.39	0.613	3.5	13.5	4.241	6.92	0.67	6.361	1.73	10.37
<i>S. mexicana</i>	1300	2000	0.013	20	60	0.167	0.179	0.42	0.425	3.5	13.5	4.241	9.98	0.35	12.270	0.82	28.88

Note: Sources of cost calculations shown in US\$: 1) labor: \$10 hourly wage; 2) seed collection: mean taken from field trials, although this will vary depending on number of source plants at a given site and degree of conservative collecting in order to maximize gene pool; 3) seed treatment: calculated from trials, includes cleaning time; 4) cost/seed: labor/collection + labor/treatment; 5) seed planting time: mean calculated from field trials; 6) total cost/site: labor/(seed sites/h) + cost/seed; 7) survival/site: taken from data; 8) seed cost/survivor: (total cost/site)/(survival/site); 9) cost/container: mean of costs taken from 3 local native plant nurseries (see Methods; included in this mean is a hypothetical low in which the practitioner collects seeds and gives them to a nursery); 10) containers/h: number of containers planted in an hour, calculated from field trials; 11) cost/site: labor/(containers/h) + cost/container; 12) survival/site: taken from data; 13) container cost/survivor: (total cost/site)/(survival/site); 14) survival ratio: container survival/seed survival, from the data; and 15) relative base cost: (container cost/survivor)/(seed cost/survivor).

^z *B. pilularis* 2 represents the survival without including the zero germination for Bobcat 1.

TABLE 6

Cost-effectiveness of containers versus seeds represented as relative cost of container/seed.

Fixed-cost amendments: cost per planting site

Species	High/low	Relative base cost	Cost/survival (container/seed)	Cost/survival seed	Irrigation	Tube	Cost/survival seed	Cost/survival	Relative cost container (container/seed)
<i>A. californica</i>	Low	24.82	0.29	7.07	0.70	1.00	1.99	8.77	4.42
	High	24.82	0.29	7.07	1.00	3.00	4.29	11.07	2.58
<i>A. rhombifolia</i>	Low	1.55	2.73	4.24	0.70	1.00	4.43	5.94	1.34
	High	1.55	2.73	4.24	1.00	3.00	6.73	8.24	1.22
<i>B. pilularis</i>	Low	6.80	0.78	5.30	0.70	1.00	2.48	7.00	2.82
	High	6.80	0.78	5.30	1.00	3.00	4.78	9.30	1.95
<i>C. betuloides</i>	Low 2 z	9.06	0.59	5.30	0.70	1.00	2.29	7.00	3.06
	High 2 z	9.06	0.59	5.30	1.00	3.00	4.59	9.30	2.03
<i>C. cuneatus</i>	Low	9.92	0.92	9309	0.70	1.00	2.62	10.79	4.12
	High	9.92	0.92	9.09	1.00	3.00	4.92	13.09	2.66
<i>C. occidentalis</i>	Low	8.37	0.51	4.24	0.70	1.00	2.21	5.94	2.69
	High	8.37	0.51	4.24	1.00	3.00	4.51	8.24	1.83
<i>F. latifolia</i>	Low	7.46	0.85	6.36	0.70	1.00	2.55	8.06	3.16
	High	7.46	0.85	6.36	1.00	3.00	4.85	10.36	2.14
<i>H. arbutifolia</i>	Low	5.82	0.78	4.54	0.70	1.00	2.48	6.24	2.52
	High	5.82	0.78	4.54	1.00	3.00	4.78	8.54	1.79
<i>P. sabiniana</i>	Low	15.47	0.51	7.81	0.70	1.00	2.21	9.51	4.30
	High	15.47	0.51	7.81	1.00	3.00	4.51	11.81	2.62
	Low	10.37	0.61	6.36	0.70	1.00	2.31	8.06	3.49
	High	10.37	0.61	6.36	1.00	3.00	4.61	10.36	2.25

Note: This cost reflects the base cost (Table 4) with the additions of common restoration amendments: tubes and irrigation. Costs were calculated as “low” and “high,” which represents the variation in rates based on personal experience and communications with restoration professionals.

z *B. pilularis* 2 represents the survival without including the zero germination for Bobcat 1.

While direct seeding was shown to be at least as cost effective as planting container stock, 2 possible alternatives to over-planting are:

1) **Over-planting within tube sites.** Because the cost of a single seed is low, adding more seeds to each tube may be considerably cheaper than adding planting sites. Thinning after germination would represent an additional labor cost but could decrease intraspecific competition. Additional experiments could test whether thinning could raise survival rates.

2) **Reducing costly fixed amendments.** Because tubes and irrigation represent a large cost, proportional to the cost of seeds or container stock, their elimination might appear to increase the cost-effectiveness of direct seeding. Without the use of tubes and irrigation, tree and shrub planting could reduce costs further by adopting the broadcast or drill-seeding techniques common to native grass restoration. Omitting these, however, might reduce seed-planting success more than container-planting success and reduce the relative cost-effectiveness of direct seeding. Future research is needed to quantify how different combinations of amendments influence realized cost-effectiveness of direct seeding and container stock across multiple species and multiple sites (and ideally, multiple years). The cost of amendments drives down the seed advantage, so in sites where these amendments can be omitted, direct seeding may be even more cost effective. Our results may be particularly applicable to restoration in semiarid and Mediterranean climates of the world (Jefferson 2004; Midoko-Iponga and others 2005; Alvarado-Sosa and others 2007; Martinez-Ruiz and others 2007). In more mesic climates, irrigation may not be necessary. In addition, the relative survival rates of seeded and container plants may vary in the absence of irrigation.

CONCLUSION

The results of this study suggest that direct seeding should be further examined as a viable technique for woody plant restoration, especially for large-seeded species. Even a modest reduction in cost can mean substantial savings when the sites, and numbers of plants, are large. Ultimately, practitioners should have a list of species and associated recommendations for planting techniques from which they make choices based on local circumstances.

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Figure 6. Toyon (*Heteromeles arbutifolia*) in tree shelter. Photo by

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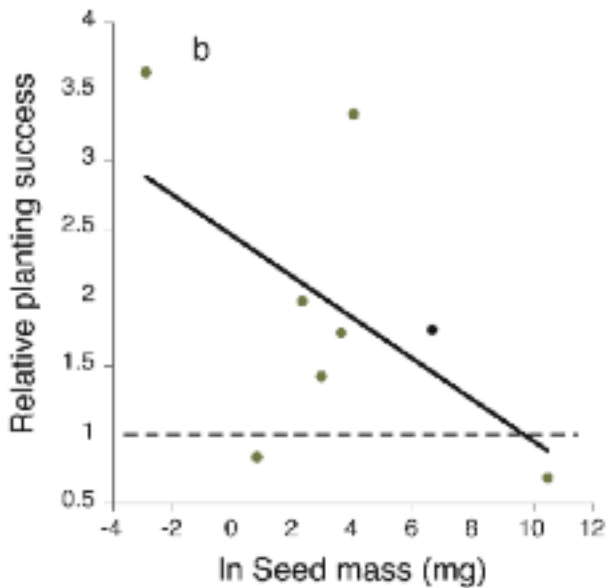
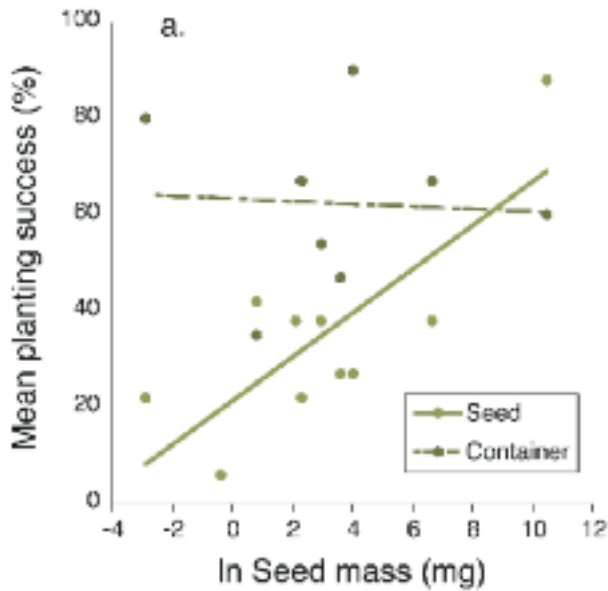


Figure 7. The relationship between mean seed size (log-transformed) and mean planting success from container stock (% success = $63.4 - 0.3 \cdot \ln$ seed size) and from direct seeding (% success = $21.3 + 4.6 \cdot \ln$ seed size) (A), and the ratio of survival from container stock divided by survival from direct seeding (ratio = $2.61 - 0.16 \cdot \ln$ seed size) (B).

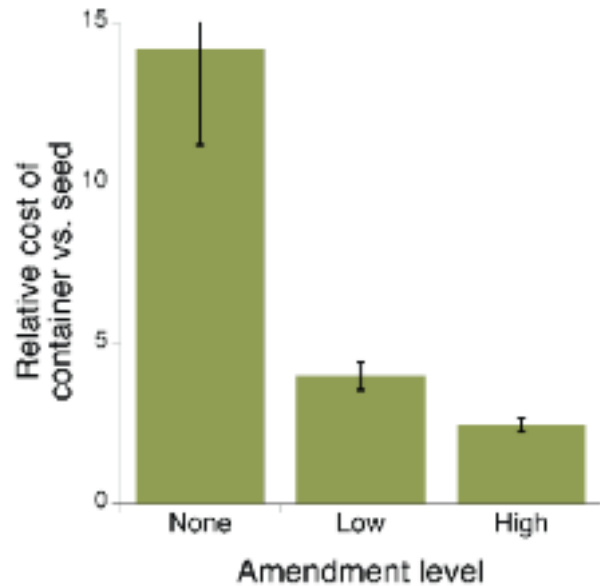


Figure 8. The ratio of the cost per survivor from container stock and direct seeded, for different amendment calculations (see Table 3), averaged across all 8 species. Bars are one standard error. Values greater than 1 (dashed line) indicate that container stock costs more than direct seeding.

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