
Container Stock Versus Direct Seeding for Woody Species in Restoration Sites[©]

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INTRODUCTION

Ecological restoration is a rapidly growing field of biology. Grassroots restoration activities have a long history and have recently increased dramatically. These are now being supplemented by state and federally sponsored restoration projects reaching tens and hundreds of millions of dollars, like those in the Everglades, Lake Tahoe, and the Sacramento River and Delta. Academic programs are blossoming nationwide. Mitigation continues to be an important "restoration" activity despite serious concerns about its environmental and scientific validity. Ecological restoration is primarily a plant science (Young, 2000). Its main activities include removal of degradative forces, soil preparation (repair), control of exotic weeds (especially in Western ecosystems), and the planting of native species. It is the latter activity that relies on expert advice from plant propagation specialists.

Plant propagation is an important part of ecological restoration. There has been considerable research on the effects of different stock sources on field performance of native woody species. In contrast, there has been only limited research comparing the effectiveness of direct seeding with the planting of container stock of woody plants, at least for nonforestry species. This research has revealed some interesting and sometimes counter-intuitive results that may have important implications for the future of ecological restoration especially as it relates to plant propagation. I will summarize some of the potential problems associated with containers and offer some future research directions.

ARGENTINE ANTS AND CONTAINER PLANTS

Argentine ants are an invasive exotic species, whose explosive spread in California is a major environmental problem. For example, the success of restoration efforts involving the endangered valley elderberry longhorn beetle (VELB) is often limited by predation from argentine ants (Huxel, 2000). Argentine ants also reduce the numbers of other invertebrates (Kennedy, 1998; Holway, 1998; Bolger et al., 2000) and even horned lizards (Suarez et al., 2000) in California. Transport through potted plants is thought to be one of the major vectors of argentine ant invasion (Holway, 1995; Hee et al., 2000). Because of this, the spread of argentine ants is most pronounced in urban

areas, where eradication and control may be difficult. In restoration sites, the presence of these ants is often a preventable disaster. It is ironic that the very container plants brought in to assist in restoration may be the source of these invasive ants. Plant material thought to be infected by argentine ants should never be used in restoration efforts. Increasingly, restoration practitioners will be asking the producers of native plant materials to be accountable with respect to this species.

COST EFFECTIVENESS OF DIRECT SEEDING VERSUS CONTAINER STOCK

There are several reasons for a preference for container stock over direct seeding. First, clients often want to see large plants as soon as possible. This is not only the case in landscaping; many mitigation plans have specific goals for plant sizes as well as densities. Container stock helps meet these requirements quickly (within the term of the contract).

More fundamentally, container stock can bypass what is often the most limiting factor in plant establishment — seed and initial seedling success. In natural populations and even in controlled field plantings, there can be large losses due to germination failure and death at the earliest seedling stages. By growing seedlings for a period of time in the greenhouse, the planted stock has already reached a stage (size) where survival is more assured.

However, this assurance comes at a cost. The longer plants are kept in containers and the larger the containers are, the greater the cost per plant. The cost effective-

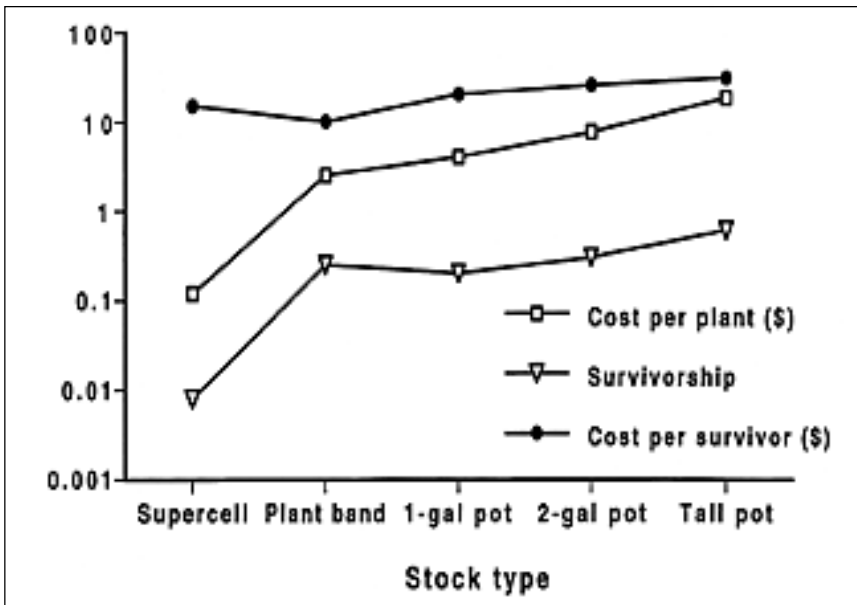


Figure 1. Cost effectiveness of different container stocks in desert restoration sites, estimated across several woody species (adapted from Bainbridge et al., 1995). Although cost per planted seedling varies over more than two orders of magnitude, cost per survivor varies relatively little.

ness of direct seeding and different types of container stock will in part depend on this relationship. In a rare examination of this in a desert restoration setting, Bainbridge et al. (1995) used experience from several woody species to estimate the cost effectiveness of a variety of increasingly costly propagation sources that had increasingly high survivorship. It appears that nature is a good agricultural economist. Although the costs per plant varied over a 300-fold range from small seedlings to large plants in tall pots in deeply augured holes, the cost per surviving plant varied over only a two-fold range (Fig. 1). In other words, the increasing costs of more intensive propagation techniques were approximately proportionate to their success in the field. Of course, a two-fold difference in cost per surviving plant is still substantial, but this analysis demonstrates that we cannot take for granted the advantages of more intensive propagation techniques.

POTENTIAL PROBLEMS WITH CONTAINER STOCK

The Bainbridge study confirms our intuition that larger plants have greater success than smaller plants. However, a small but growing number of studies suggest that container plants may not always have greater success than seeds. It appears that in a wide variety of woody species, individuals originating from seed on site perform better than individuals transplanted as container stock.

Halter et al. (1993) found that even after 11 years, lodgepole pines (*Pinus contorta*) transplanted as 1-year-old seedlings were growing more slowly than trees that regenerated naturally at the same site (Fig. 2). Their root excavations showed major root deformations in trees from container stock. Most striking was the lack of deep roots, although lateral support roots also suffered from container growth.

McCreary has been examining the success of blue oaks (*Quercus douglasii*) planted using different stock and different maintenance. Although 1st year survival was greater in container stock than from acorns, thereafter, survivorship was similar and growth rates were significantly higher in oaks planted as acorns (Fig. 2b). These results come from separate experiments not designed to test these differences directly, but there are no reasons to believe that they are not real.

Welch (1997) planted both 1-year-old container seedlings and seeds of big sagebrush (*Artemisia tridentata*) in seed increase gardens under natural soils and rainfall regimes, but with weed control. Plants grown from seed had greater survivorship, greater growth, and greater reproductive output than plants grown from container stock. The difference in growth rate was so great that after just 4 years, plants grown from seed were significantly larger than plants grown from container stock, even though the latter had a year's head start in the greenhouse.

These above-ground differences were correlated with below-ground differences. Plants grown from seed had greater root biomass, greater root-shoot ratios, greater maximum rooting depth, and shallower minimum rooting depth than plants transplanted from containers (Fig. 2c). As in the pines of Halter et al. (1993) excavations revealed a loss of taproots in container stock.

Marshall and Gilman (1997) examined the roots of live oak (*Q. virginiana*) that had been either field-grown or container-grown prior to transplantation. They also found the field-grown stock had greater root mass at both shallow (0 to 25 cm) and deep (75 to 100cm) horizons, but not at intermediate depths. The roots of container-grown stock, but not field-grown stock, suffered in unirrigated plots. In a similar study, Gilman and Beeson (1996) examined young laurel oaks (*Q.*

laurifolia) and East Palatka holly (*Ilex x attenuata*) that had been either field grown or container grown prior to transplantation. For both species, the field-grown plants had greater height, above- and below-ground biomass, and greater rooting depth than container-grown plants.

Prompted partly by these results, we have begun a study of factors affecting the success of valley oak seedlings (*Q. lobata*) in the field (Young and Evans, in prep).

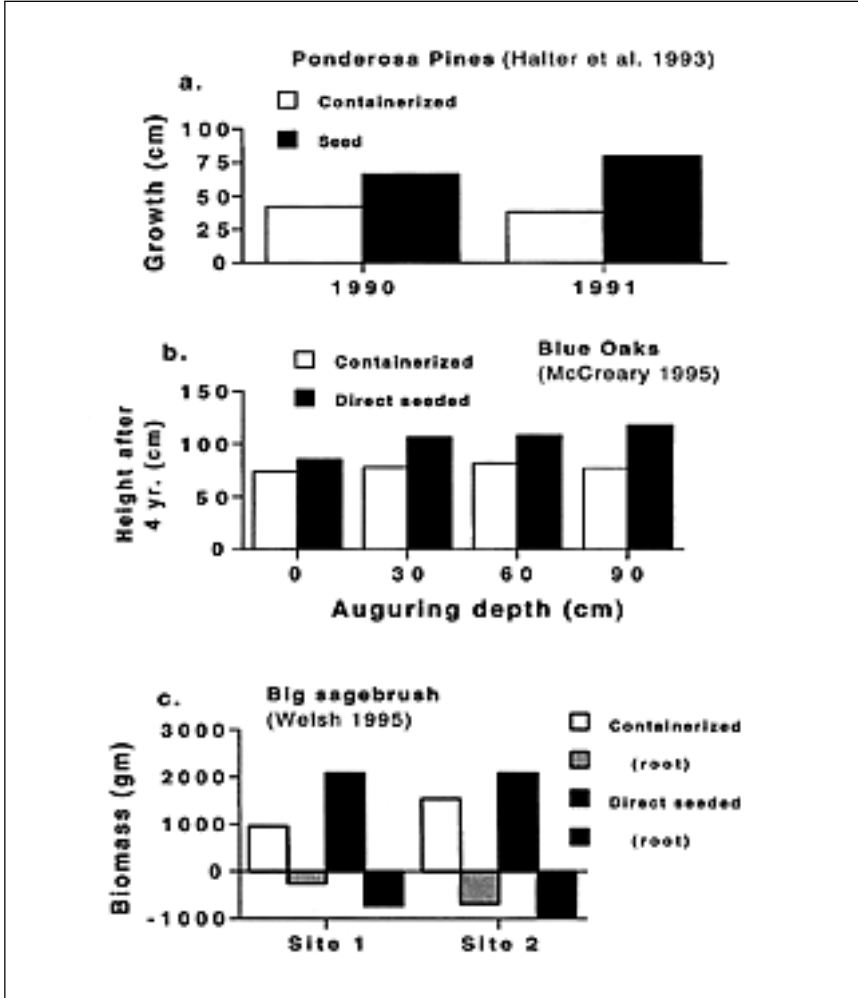


Figure 2. Greater vigor of plants grown from seed compared to those planted from container stock. (a) Growth in ponderosa pines ten and 11 years after planting (adapted from Halter et al. 1993). (b) Height of blue oaks 4 years after planting (adapted from McCreary, 1995). (c) Above- and below-ground biomass of big sagebrush 3 years after planting (adapted from Welsh, 1997). Note not only greater root biomass of directly seeded plants, but also their greater root-shoot proportions. See the original papers for details and statistics.

We used three kinds of container stock: (1) 1-year-old seedling grown in larger containers, (2) 3-month-old stock grown in smaller containers, and (3) 3-month-old stock started in smaller containers, and transplanted to larger containers after 7 weeks. We planted these into a field setting, along with direct seeded acorns. We have also been manipulating irrigation methods as part of a larger study examining how horticultural practice affect plant success in restoration settings. As in most of the studies reviewed here, the field sites had natural soil and rainfall, but some weed control.

Our initial results parallel the others outlined above. Although acorns suffered greater initial losses, the survivors' growth rates were similar across all seedling sources. In irrigated plots, later survivorship was similar across seedling sources, but in unirrigated treatments, the oaks grown from field-sown acorns had significantly greater survivorship in the first year than did the container stock, suggesting that direct-seeded oaks had greater ability to withstand drought than did container stock (compare the results with live oak, above).

Across all of these studies, there was the tendency for direct-seeded plants to perform better than container transplants. There are at least three possible reasons for this — transplant shock, lack of (drought) hardening, and root deformation. Given that many of these differences were expressed months and even years after transplantation, it appears that short-term transplant shock is an unlikely explanation.

Plants growing in dry condition adjust in a number of ways. They produce smaller leaves, fewer stomates and relatively more root biomass and may adjust transpiration behaviors and physiology. Seedlings initially grown in greenhouses would be expected to have expressed fewer of these adaptive traits and may be "caught out" when planted into dry field sites. Such effect would be due to the greenhouse environment itself and perhaps largely independent of container growth per se (although virtually all greenhouse stock is grown in containers). Again, we might expect these effects to be relatively transitory, even if they may linger longer than transplant shock effects.

Root deformation effects, however, can last throughout a plant's lifetime. The root deformations reported by Halter et al. (1993) were still readily evident 11 years after planting. Moore (1987) suggests that once a taproot is lost in a container, it is unlikely to be replaced regardless of how it is planted out. We have previously shown (Hobbs and Young, in press) that taproots rapidly reach the bottoms of even large containers in a greenhouse setting. If so, then even a relatively short period of time in a container may put many woody plant species at considerable risk when planted into restoration sites.

FUTURE RESEARCH

Plant propagation expertise is likely to be increasingly directed to application in ecological restoration. The effectiveness of this expertise will depend on our ability to address the specialized requirements for the plant material used in restoration. This review suggests several lines of future research:

- For a given species, is direct seeding or container stock transplanting a better technique for field establishment?
- For a given species, does the answer differ depending on site conditions, stock type, or planting technique?

- Across species, are there patterns that will allow us to predict which species are more likely to benefit from container propagation? For example, are tap-rooted species more likely to suffer deleterious effects of being grown in containers?
- What methods can be used to improve the survival rate of both transplanted and direct-seeded plant materials at restoration sites?

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