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Review

Characterizing the Utility of the Root-to-Shoot Ratio in Douglas-Fir Seedling Production

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Abstract: Nursery-grown tree seedlings are a vital component of successful restoration and reforestation programs, useful when calls for increased planting for industrial forest management are made, and a tool for climate change mitigation. One of the most extensively planted and studied trees in Western North America is Douglas-fir. Building on that body of work, this review was conducted to identify if the root-to-shoot ratio (root:shoot, R:S), a commonly referred-to metric in reforestation planning, yields meaningful guidance for producing seedlings that are better able to establish across a variety of field conditions. The results indicated that there is wide variability in R:S of nursery-grown seedlings. The relationship between R:S and subsequent root growth and seedling survival varies depending on Douglas-fir variety, seedling stocktypes, and site conditions. The biological and physiological basis for using R:S remains, and likely could be used to enhance seedling quality; however, there is an ongoing need for planning and collaboration between researchers and practitioners to identify how to best deploy this evaluation tool.

Keywords: biomass allocation; field establishment; plant hydraulics; seedling quality

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1. Introduction

Planted seedlings are a key part of many reforestation plans, including environmental restoration and efforts to address climate change [1]. To be effective in these projects, seedlings must survive the transition from the nursery to establishment in the field [2]. There is a strong impetus to ensure the performance of planted seedlings, given that there are over a billion seedlings being grown in forest nurseries in the United States for reforestation and restoration [3] and global commitments to restore and expand forest cover [4]. To that end, the Target Plant Concept was developed as a framework to guide the successful establishment of nursery-grown seedlings [5].

One aspect of the Target Plant Concept is to identify quantifiable morphological and physiological seedling attributes which ensure establishment success. In practice, nursery professionals look for specific morphological metrics to guide seedling production, with species and outplanting context in mind. However, defining specific attributes that correlate with survival quickly is complicated. Assessments of seedling quality need to capture the capacity of the seedling to survive under limiting environmental conditions, rather than optimum conditions [6]. Nursery production regimes manipulate seedling growth and physiology using environmental conditions and the timing of production cycles [7,8]. Stocktype decisions, container size, levels and types of fertilization, irrigation regimes, chemical and biological properties of growing media, and many other factors influence seedling growth [9–14]. In the field, silvicultural treatments, vegetation management, microenvironments, planting quality, and seedling size and structure at planting (i.e., stocktype) impact seedling survival and growth [15,16]. Therefore, it is challenging to define quantifiable morphological attributes with enough specificity to be useful to nursery professionals, while also allowing for the variability in attributes necessary to accommodate different outplanting environments.

With this challenge in mind, we sought to explore reported values of one morphological attribute, the root to shoot ratio (R:S), in the context of one species, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), to answer the question of whether R:S can be quantified and linked to outplanting success. Nursery professionals and foresters have turned time and again to the idea of ratio of the root biomass to the shoot biomass (R:S) as a quality standard for nursery-grown seedlings [17]. We use the following definition of R:S: "Total plant root system mass or volume divided by the total shoot system mass or volume, usually on an oven-dry basis, sometimes on a fresh weight basis" [18].

$$\frac{Root\ mass\ (g)}{Shoot\ mass\ (g)} = root : shoot\ ratio \tag{1}$$

If the seedling has more root biomass than shoot biomass, the ratio is greater than one; if there is more shoot biomass to the seedling than root biomass, the ratio is less than one.

R:S is intended to indicate a morphological balance within a seedling to absorb water through the roots and resupply the aboveground portion as moisture is lost through evapotranspiration. The assumption is that a well-balanced seedling is prepared to survive outplanting [19]. There is an ecological basis for assuming that R:S of a seedling indicates its capacity to survive specific conditions at outplanting. When planted seedlings face challenging environmental conditions, such as dry soils and high evaporative demand, having adequate root function to supply the aboveground portion with sufficient water is critical for growth and survival [20]. However, the usefulness of the R:S as it relates to seedling quality and prediction of seedling survival is debated [19,21–23]. When literature reviews examine a variety of species, stocktypes, and outplanting environments, the outcomes are inconclusive as to whether the attribute of R:S can be linked to outplanting success. Species are known to use different strategies to persist under the same conditions, so it is likely that different species should have different target R:S.

Specific published recommendations for R:S in nursery production vary, stating that it should be as high as possible [24], that R:S of 1:2 is desirable [21], or that it should be 1:2 or more for container stock and 1:3 or more for bareroot stock [25]. Some studies examining specific conditions found clear relationships between R:S balance (0.8 to 1.3) and survival, such as for Douglas-fir and ponderosa pine on dry sites in north-central Washington [26]. However, other work found that seedlings with similar R:S, 1.5 to 1.7, represented the best and worst surviving among a variety of tested stocktypes [27]. Even when specifically considering R:S of container-grown conifer seedlings facing dry conditions after planting, the ratio did not appear to be a predictive metric [21].

We wanted to know if a focus on a specific species could reveal more useful conclusions about R:S. Given the evidence of adjustment to environmental conditions, the physiological mechanisms that dictate biomass allocation, and the persistence of the concept of R:S in the nursery literature as a way to communicate balance within seedlings, we sought to define the range of R:S in Douglas-fir seedlings, refine morphological targets for nursery growers, and further examine how R:S relates to seedling performance after planting. Douglas-fir is one of the world's premier timber species, and its planting and early-stand silviculture have been studied for decades [28]. If an appropriate R:S is apparent in any species, the amount of research that has been conducted on Douglas-fir seedlings might reveal informative ratios.

This work was intended to address the following questions:

Is there an inherent R:S value for Douglas-fir seedlings?
Is there a consistent R:S to which Douglas-fir seedlings are grown in bareroot and container systems?
Do Douglas-fir seedlings align with a consistent R:S after transplanting?
Does the starting R:S value correlate with survival after transplanting?

Answering these questions could help define the desirable R:S value of nursery-grown Douglas-fir seedlings.

2. Materials and Methods

We searched for published journal articles in two databases using keyword searches. In the first, Web of Science, we used the terms "Douglas fir" OR "*Pseudotsuga*" AND "root*" to search for articles published between 1967, the earliest year in the database, and March 2019. We intentionally searched for broad terms, because we were looking for published data on root and shoot biomass, even in cases where the article did not explicitly discuss the seedlings' R:S. Searches that also included "shoot" OR "top" failed to capture articles that were known to have the type of data we sought, so we did not further limit the search by these terms. The second database used was Treesearch, an online system of the publications authored by U.S. Forest Service scientists. The database compiles peer-reviewed work published by the agency. Within Treesearch, we limited the search to general technical reports, research papers, and research notes because journal articles had already been represented in the Web of Science database. In cases where an experiment was published as both a report and a scientific journal article, data from the journal article were used. Conference abstracts were not included.

We evaluated titles and abstracts of the resulting studies for inclusion based on whether a study met the following criteria: (1) measured individual Douglas-fir trees, even if the data were reported as means for a sample of seedlings, and (2) reported R:S or biomass data for roots and shoot. For this review, we were not interested in studies that primarily focused on forest ecosystem dynamics, including community-level belowground biomass; papers on tree disease or mycorrhizae (unless used as a nursery amendment); or papers that reported only aboveground growth. If R:S was not reported, but root and aboveground biomass were, we calculated the ratio (Equation (1)). For data reported only in a figure, we used the web version of WebPlotDigitizer to extract the values [29]. We recorded relevant information on seedling subspecies, average total biomass, age, stocktype, history of planting, and growing environment to the extent that it was available.

In addition to summarizing the collected data, we conducted the following statistical analyses using R version 4.0.2. We used a one-sided t-test to test whether nursery production regimes resulted in seedlings that matched the recommended R:S by stocktype. For the remainder of the analyses, we tested for correlations using a Pearson's coefficient. Given that the data were drawn from a range of experimental and field conditions, we wanted to determine whether there was a relationship between the variables of interest. Where data were relevant to the question of interest and there were sufficient data to test correlations, we subset the data by variety and production method: container or bareroot.

3. Results

From the two databases, 185 articles and reports were found to have published biomass data for Douglas-fir seedlings. Of these, 79 were dropped from our analysis for having unclear graphs or tables, reporting R:S on an area basis rather than an individual tree basis, or not providing sufficient biomass data to calculate R:S. The published work represented a wide variety of experimental and field conditions, two varieties of Douglas-fir (var. *menziesii*, or coastal, and var. *glauca*, or interior), and bareroot and container stocktypes and naturally-established seedlings. Each experimental treatment or observation group that was reported within each article was a data point in our analysis.

Figure 1 shows the variability of published Douglas-fir seedling R:S values plotted against seedling biomass on a log scale. The mean R:S for seedlings that started as container stocktypes across all other variables was 0.61 (range = 0.20 to 2.76, sd = 0.32, n = 493). For seedling that started as bareroot stocktypes, the mean R:S was 0.60 (range = 0.12 to 1.74, sd = 0.29, n = 214). Interior seedlings (var. *glauca*) had a mean R:S of 0.57 (range = 0.12 to 2.18, sd = 0.35, n = 225). Coastal seedlings (var. *menziesii*) had a mean R:S of 0.61 (range = 0.19 to 2.76, sd = 0.31, n = 508).

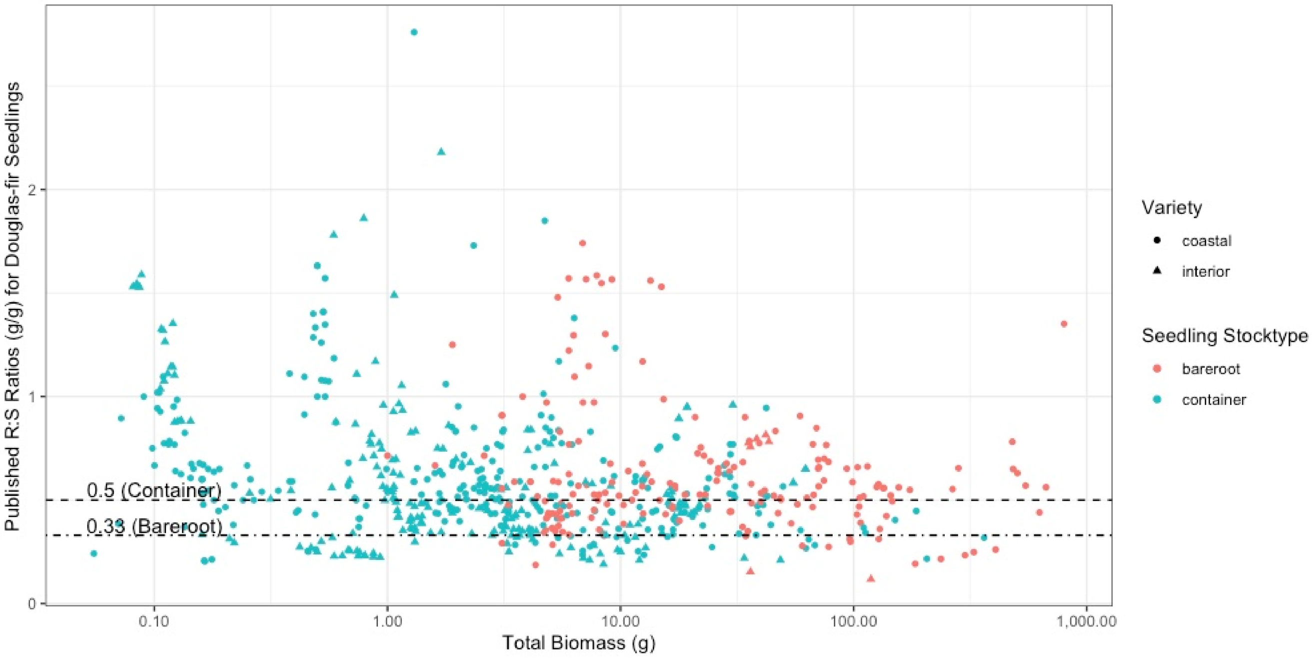

Figure 1. Average R:S by seedling size from published Douglas-fir seedling research. Total seedling biomass is on a log scale. The line at 0.5 represents the minimum R:S standard for container seedlings; at 0.3 is the minimum R:S standard for bareroot seedlings [25]. Seedling stocktype is given by color and subspecies is indicated by shape. Adapted from [30].

We found several published R:S values for naturally-established and direct-seeded Douglas-fir seedlings in forest environments. The R:S in 4 to 6 year-old naturally-established seedlings was 0.31 (n = 14) [31]. The R:S values in direct-seeded seedlings were 0.23 to 0.35, 0.13 to 0.20, and 0.26 in their first, second, and third years, respectively (n = 55) [32]. In a different direct-seeding experiment, R:S was 0.50 to 0.75 (n = 36) [33].

The variability in R:S occurs across different seedling sizes. The median total oven-dry biomass was 4.2 g. Surveying the seedlings with total biomass within 1 g of median, R:S ranged from 0.18 to 1.85. At the minimum R:S in this range, 0.18, the root contributed 0.68 g and the shoot 3.64 g to the total biomass of 4.32 g. This was an average R:S for a group of bareroot 1 + 1 seedlings (var. menziesii) measured 6 months after transplanting into a field [34]. At the other end of this range, for R:S of 1.85, the roots weighed 3.07 g and the shoot 1.66 g for a total biomass of 4.73 g in a group of seedlings (var. menziesii) raised in 8-L containers over 2 years for an experiment testing the effects of soil type on growth [35]. For the smallest seedlings in the dataset, average total dry biomass was 55 mg (R:S = 0.25) [12], and for the largest seedlings, measured three years after planting 1 + 0 bareroot stock, average total dry biomass was 800 g (R:S = 1.3) [36].

For the subset of the data that reported R:S of seedlings produced through standard nursery regimes, before transplanting in the field, we wanted to know if seedlings were grown to the recommended R:S value, using [25] as the standard. This dataset included experiments that compared different nursery treatments. The recommendation for bareroot seedlings is 0.33; in the collected studies, bareroot seedlings were grown to a mean R:S of 0.52 in nursery production, significantly greater R:S than recommended ($p < 0.01$; 95% confidence interval: 0.49 to 0.56; n = 93). For container seedlings, the recommended R:S is 0.5. Within these data, container seedlings were grown to a mean of 0.53, which is not significantly different from the recommendation (p = 0.10, 95% confidence interval: 0.50 to 0.56; n = 123). The most common types of studies on impacts of nursery practices were container size or spacing (163 values), fertilizer use (120 values), and mycorrhizae amendments (81 values). Not all studies reported R:S before transplanting into experimental treatments, so not all were included in the preceding analysis.

To test the relationship between the time to produce a bareroot seedling and the resulting R:S, we computed a Pearson's correlation coefficient (Figure 2). There is a negative correlation between the years a seedling grows in a bareroot nursery and R:S (R = −0.39, $n = 93$, $p < 0.01$). The stocktype number describes the number of years seedlings spend in their first stage of the production cycle, given before the "+" sign, and then the number of years seedlings spend in the second stage of the production cycle after transplanting. For example, a 1 + 1 seedling was grown for one year, lifted, graded, and transplanted, and then grown for a second year. The most commonly-reported stocktype in these data are 2 + 0 seedlings. Bareroot values were all of the coastal variety or the variety was not reported, but assumed to be coastal because of the locations the seedlings were grown in.

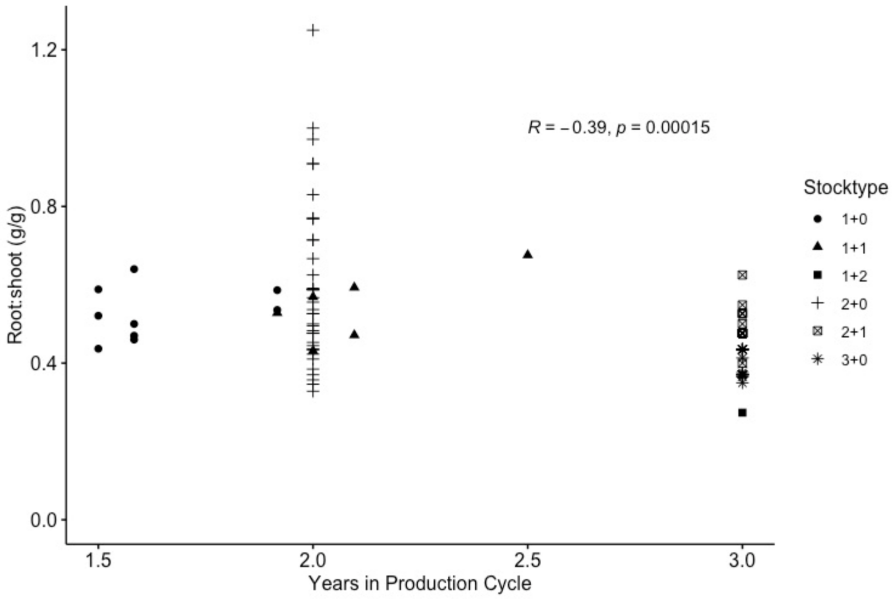

Figure 2. Relationship between R:S and the time to produce coastal Douglas-fir bareroot seedlings. Stocktype is indicated by shape and further described in the text. There is a negative correlation between the years a seedling grows in a bareroot nursery and R:S (R = −0.39, $n = 93$, $p < 0.01$).

To test whether container size is related to resulting seedling morphology, we again computed a Pearson's correlation coefficient (Figure 3). We tested the two varieties separately. There is no correlation between container volume and R:S for seedlings of either the coastal variety (R = −0.08, $n = 67$, $p = 0.55$) or the interior variety (R = −0.22, $n = 56$, $p = 0.10$). The most commonly-used container volume in the published research was 336 mL, which corresponds to a Styroblock 45 (Beaver Plastics, Acheson, AB, Canada).

To test if there is a relationship between time since planting and resulting R:S, we calculated Pearson's correlation coefficient for seedlings, grouped by coastal and interior varieties (Figure 4). Within this dataset are seedlings that were transplanted into field, common garden, and pot experiments, though we only included pot experiments where the growing container was large enough to not substantially limit root growth. Data were not analyzed separately by stocktype because there are not enough reported values from interior bareroot seedlings. There is a significant negative relationship between time since planting and R:S in coastal seedlings (R = −0.18, $n = 287$, $p = 0.004$). There is a significant positive relationship between time since planting and R:S in interior seedlings (R = 0.61, $n = 85$, $p < 0.001$). For studies that explicitly considered transplanted seedlings, the impact of site preparation methods was a common theme (51 values).

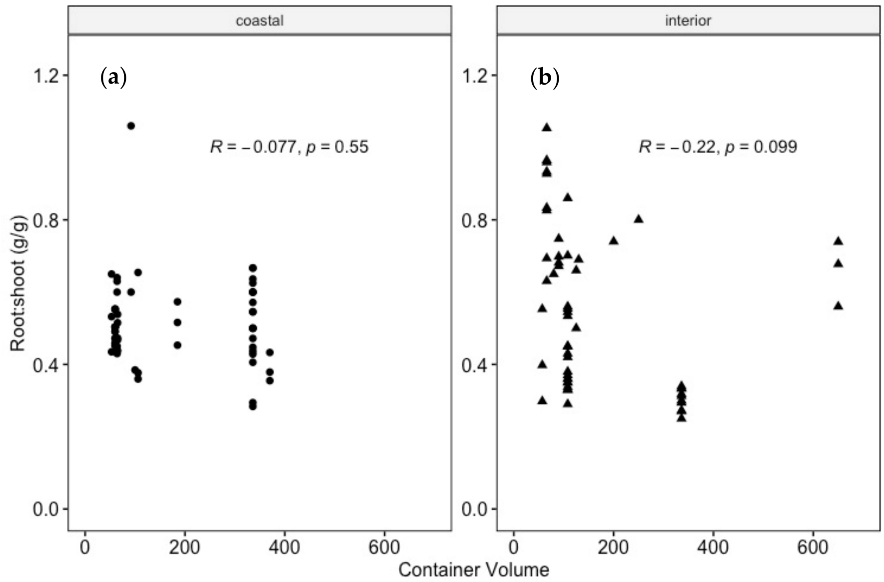

Figure 3. Relationship between R:S and container volume in which the seedlings were grown for Douglas-fir seedlings of the (**a**) coastal and (**b**) interior varieties. There is no correlation between container volume and R:S for seedlings of either the coastal variety (R = −0.08, n = 67, p = 0.55) or the interior variety (R = −0.22, n = 56, p = 0.10).

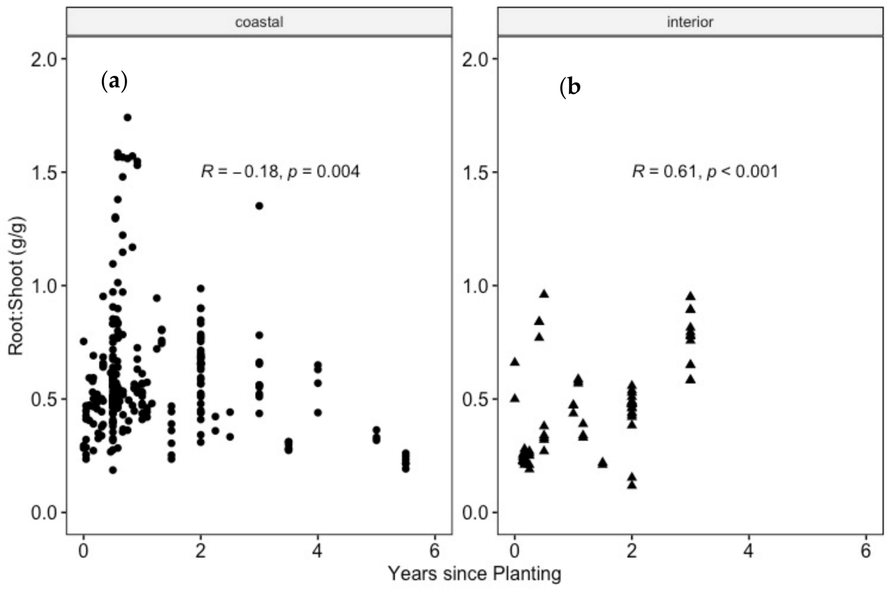

Figure 4. R:S after planting for Douglas-fir seedlings of (**a**) the coastal and (**b**) interior varieties. There is a significant negative relationship between time since planting and R:S in coastal seedlings (R = −0.18, n = 287, p = 0.004). There is a significant positive relationship between time since planting and R:S in interior seedlings (R = 0.61, n = 85, p < 0.001).

We computed Pearson's correlation coefficients to assess the relationship between R:S at planting and subsequent survival for both bareroot and container seedlings (Figure 5). The timeframe on which survival was assessed varied by study. For bareroot seedlings, there was a negative correlation between R:S at planting and survival (r = −0.31, n = 93, p = 0.002). These data were taken from five papers with published survival of bareroot seedlings. For container seedlings, there was a positive correlation between R:S at planting and survival (r = 0.61, n = 14, p = 0.02). These data came from four papers that published survival of container seedlings. Survival data were only available for seedlings of the coastal variety.

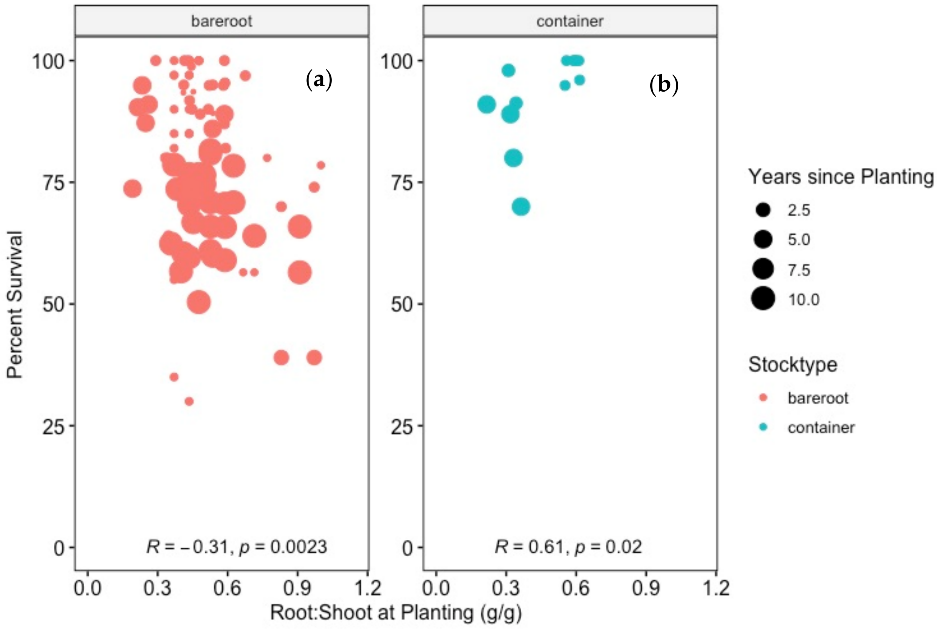

Figure 5. Initial R:S and survival after planting for coastal Douglas-fir seedlings that were (**a**) bareroot or (**b**) container stocktypes. The timeline on which survival was assessed is indicated by the size of the datapoint.

4. Discussion

The aim of this review was to determine if there were answers to the following questions among the published R:S values for Douglas-fir seedlings. If there are satisfactory answers, they can be used to quantify the R:S for Douglas-fir seedlings, which relates to outplanting success.

4.1. Is There an Inherent R:S Ratio for Douglas-Fir Seedlings?

Figure 1 demonstrates that there is a wide variety of R:S outcomes for Douglas-fir seedlings. This is a result of the variety of seedling sizes, nursery cultural practices, and outplanting environments considered within the literature review. Nursery production manipulates R:S through pruning and other practices, as discussed in more detail below. In the limited sample of direct-seeded and naturally-established seedling there was no suggestion of a "natural" R:S for Douglas-fir. From these data, there is not a clear, single R:S that should be the standard target to which all Douglas-fir nursery seedlings are grown.

4.2. Is There a Consistent R:S to Which Douglas-Fir Seedlings Are Grown in Bareroot and Container Systems?

Bareroot seedlings are grown to exceed the recommended R:S of 0.33. The result that bareroot stocktypes which take longer to produce have lower R:S is likely a product of the nursery growing regime. The bareroot growing process reduces root structure when lifting seedlings from nursery beds and when pruning root systems, while leaving the aboveground portion of the seedling intact. This will make the R:S skew lower for older, larger seedlings. The mean R:S for container seedlings matches recommended R:S (0.5); given that these are means, approximately half the seedlings in the dataset have smaller R:S than the recommendation. However, with no significant relationship in R:S among container sizes, this suggests seedlings maintain balance across different container sizes. This is likely the result of proactive control of seedlings growth through production practices, such as reducing irrigation to slow height growth and encourage root growth towards the end of the growing season. Nursery-grown seedlings are generally being grown to match or exceed the minimum recommended R:S; however, the published values do not provide enough performance-based information to update the recommendations to include optimal ranges for R:S

4.3. Do Douglas-Fir Seedlings Align with a Consistent R:S after Transplanting?

There was a difference between the two Douglas-fir varieties in the relationship between R:S and time since planting. Coastal seedlings grow more aboveground biomass relative to belowground biomass, resulting in lower R:S as more time passes since planting. For interior seedlings, the relationship is opposite, with higher R:S over time (five to six years after planting). Interior seedlings originate from and are planted in more xeric environments [37]; the positive trend in R:S after planting may indicate a growth response to dry conditions [38]. However, more work needs to be done to link root growth after planting to environment conditions, especially soil water availability. These results raise the question of whether nursery-grown seedlings should be (1) grown to match the predicted R:S that seedlings will attain at the outplanting site, or (2) grown to address limiting factors at outplanting, e.g., with an intentionally high R:S to allow for some root loss with storage, transport, and planting. Answering these questions will require additional research.

4.4. Does Starting R:S Correlate with Survival after Transplanting?

Surprisingly, there is a negative relationship between R:S at planting and survival for bareroot seedlings. This is counter to assumption that more roots are always better [24]. Still, there are high rates of survival (>80%) for a range of starting R:S among bareroot seedlings. Again, the bareroot nursery regime likely contributes to lower starting R:S on some seedlings. The relationship between starting R:S and survival is positive for container seedlings. Among these data, there is not a R:S that guarantees Douglas-fir seedling survival after planting.

There are several caveats to address regarding the data in our analyses. The data represent seedling metrics reported for nursery research, not standard nursery production. Given that the median oven-dry biomass of seedlings in data set is 4.2 g, these experiments were often working with seedlings that were smaller than full-sized nursery seedlings. In some cases, seedlings were graded and culled based on size standards within the experiment and so did not represent the entire range of seedling sizes, though this also happens with nursery production. Seedlings with extreme R:S are likely excluded from both research and field planting. Research papers on topics other than nursery production (e.g., field survival, etc.) often did not use standard container sizes or report the bareroot stocktype for seedlings used in experiments. Survival data are underreported, especially linked to starting R:S. Though a simple method, different approaches to determining R:S can cause variability. Smaller seedlings especially will be strongly impacted by slight changes in allocation. However, it would be possible to move past these caveats with careful attention to the research process and recordkeeping. Millions and millions of Douglas-fir seedlings are grown using a variety of methods each year and planted across a breadth of environmental conditions, so there is no shortage of real-world outcomes to track. It would require a coordinated effort to measure and monitor seedlings to build a more complete dataset.

In all future work related to seedling R:S, it is possible to improve on the experimental design, methodology, and communication of the results to refine our understanding of R:S and how it can be used to improve seedling production in nurseries. For example, researchers are advised to:

- Measure R:S at the onset of the project to establish a baseline, and after the implementation of experimental treatments,
- Include survival data, whether or not that was the primary focus of the research project, to help with the interpretation of R:S,
- Report the timeframe in which changes in R:S are considered, and

- Clearly communicate the methods used to measure and calculate R:S, and the total size of the seedlings measured.

Following these recommendations will help us better apply seedling research outcomes to questions about seedling production and survival after planting.

There are also additional approaches for quantifying and understanding root function. A key challenge to linking R:S to outplanting performance is that this metric is a proxy measurement. The ratio of root biomass to shoot biomass is intended to indicate how well the belowground part of the plant can provide water and nutrients to the aboveground portion. However, proxy measurements are only as good as the validity of their underlying assumptions. Additionally, roots have multiple functions. They are important not only to supply water to the shoot, but also to anchor the plant, store carbon, and establish mycorrhizal associations [39]. We can refine R:S as a proxy measurement and update the underlying assumptions by taking advantage of recent progress in the fields of plant hydraulic physiology and plant imaging.

Plant hydraulic physiology is the study of water movement through plants [40]. The methods used in hydraulic physiology research offer direct ways to measure water movement through the plant, from the roots to the aboveground portion [41]. The field of plant hydraulic physiology has also developed methods to scale the supply of water to the leaf area of a plant, directly linking water supply to water demand [42,43]. There are also models of plant hydraulic physiology that use metrics such as height, rooting depth, and other morphological attributes-data that already tracked in nursery production- to predict water supply and demand [44]. Adapting these models specifically for nursery seedlings would directly link R:S to plant hydraulics.

A second opportunity for improving on the study of R:S is to take advantage of advances in imaging technology and computing power. The R:S essentially disregards any question of root architecture and arrangement, which may be limiting its applicability to questions of plant performance. In-situ root imaging has been accomplished with technologies such as MRI, CT, and 3D scanning [45]. Transparent growing media and technologically-advanced rhizotrons offer new ways to tracking root growth over time [46].

It is important to keep in mind that simply more data will not solve all problems related to roots on nursery-grown seedlings. We have demonstrated in this paper that having lots of reported values for Douglas-fir seedlings still does not answer basic questions about optimal targets for root systems. Root system analysis will still need to be linked to practical outcomes of seedling performance, just like any other seedling metric [47]. For example, a researcher could use new imaging tools to investigate whether a practice such as undercutting roots in a bareroot nursery leads to more fibrous root systems, as quantified by a high-definition 3-dimensional scanning. A follow-up study could use tools from plant hydraulic physiology to compare water movement through root systems with varying amounts of fine roots, then model root hydraulic conductance in terms of plant performance and survival at planting sites. Linking root traits to plant physiology and ecosystem processes is an ongoing topic of study [48].

This review demonstrates the tension between specificity and variability in defining a morphological metric such as R:S. On the one hand, the metric needs to be precise enough to be practical and helpful for guiding nursery professionals in seedling production. On the other hand, there needs to be flexibility and nuance regarding how the metric relates to environmental conditions at outplanting. Morphological targets, such as R:S of 0.5, may be most useful as broad guidelines rather than prescriptions for nursery production. The target defines a range within which seedlings are most likely to be successful and the limits beyond which they are unlikely to survive. To get more specific answers on the attributes that determine outplanting success, we will need include additional information, such as outputs from physiological models of water movement and measurements of soil water availability at the outplanting site. Even for a very well-studied species such as Douglas-fir, there is not a one-size-fits-all answer to the metric of R:S.

5. Conclusions

Although R:S has not met expectations for defining nursery quality metrics, it is still useful. That there is a balance in seedling biomass allocation is supported by work from forest ecology and plant physiology. Despite the methodological issues with R:S, and the lack of predictive power found in the metric based on this and past reviews, it is not a metric that is likely to, or even should, be retired. However, there are steps that can be taken to refine the conversation around R:S, and new research directions that can further our understanding in the context of plant hydraulics and other elements of physiology. R:S remains useful a simple description of seedling balance, underlain by physiological explanations, but it cannot be the endpoint in discussions of seedling quality or growth targets. As we are faced with the challenges of climate change and deforestation, on top of the existing shortcomings in seedling survival for reforestation and restoration, we need to improve seedling survival by understanding the interactions among seedling morphology, physiology, and environment.

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