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Review

Seedling Quality: History, Application, and Plant Attributes

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Abstract: Since the early 20th century, silviculturists have recognized the importance of planting seedlings with desirable attributes, and that these attributes are associated with successful seedling survival and growth after outplanting. Over the ensuing century, concepts on what is meant by a quality seedling have evolved to the point that these assessments now provide value to both the nursery practitioner growing seedlings and the forester planting seedlings. Various seedling quality assessment procedures that measure numerous morphological and physiological plant attributes have been designed and applied. This paper examines the historical development of the discipline of seedling quality, as well as where it is today. It also examines how seedling quality is employed in forest restoration programs and the attributes that are measured to define quality. The intent is to provide readers with an overall perspective on the field of seedling quality and the people who developed this discipline from an idea into an operational reality.

Keywords: seedling quality; historical perspective; morphological attributes; physiological attributes

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1. Introduction

Forest restoration is a complex process that requires many steps to ensure successful forest establishment. These steps include choosing suitable tree species and provenance, applying nursery cultural practices to produce quality seedlings, ensuring proper seedling handling practices, and making site modifications to improve the physical environment of the restoration site [1,2]. Implicit within a seedling production program is the recognition that inherent species attributes [3] and phenotypic traits created during nursery culture [4] are both important in determining initial seedling field performance. Thus, seedling quality is a critical component in ensuring a successful forest restoration program.

This review summarizes the evolution of seedling quality from three perspectives. First, a historical perspective outlines a timeline for the evolution of this discipline over the past century. Second, the application of seedling quality within restoration programs is discussed from the perspectives of monitoring the process and monitoring the product. Third, various plant attributes that have been considered or are currently in operational use for defining seedling quality are discussed. The intent of this review is to provide nursery practitioners and foresters with a better understanding of seedling quality so they can effectively apply these assessment practices in their forest restoration program.

2. Historical Perspective on Seedling Quality

The focus on seedling quality in forest restoration programs goes back at least a century (Table 1). Since the early 20th century, silviculturists have recognized the importance of planting seedlings with desirable attributes, and that successful establishment was associated with these attributes [5]. Early on, foresters examined plantation failures in an attempt to discern causes of poor performance, because of the silvicultural investment needed to ensure seedling establishment (e.g., [6–9]). Often, poor performance was attributed to environmental stress, animal grazing, or damage from disease or insects. However, poor-quality seedlings [8] and the inability of planted seedlings to grow roots [9] were also suggested as probable causes of plantation failure. Thus, these early researchers began to ask questions as to how best to grow quality seedlings and what plant attributes influence seedling survival and growth (i.e., field performance) after planting on reforestation sites. Furthermore, studies initiated on southern pines in the 1930s [10,11] were groundbreaking, in that they showed that seedling attributes measured at the end of nursery culture were related to subsequent seedling field performance.

Table 1. A chronological list of references that discuss seedling quality, review seedling quality issues, or provide conceptual ideas related to seedling survival and/or growth after outplanting.

Author(s)/Date	Relevance to the Discipline of Seedling Quality
Toumey (1916) [5]	Desirable seedlings are selected for their “vigor and growing power”
Kittredge (1929) [8]	Poor-quality planting stock is defined as the reason for plantation failure.
Wakeley (1935) [12]	Higher morphological (i.e., shoot and root length, diameter) grades of seedlings showed “consistent superiority” over lower grades of seedlings.
Rudolf (1939) [9]	The inability of planted seedlings to grow roots is defined as the reason for plantation failure.
Wakeley (1948) [10]	“Grades applied to nursery stock can be useful only so far as they distinguish seedlings with a high capacity for survival and growth after planting from those with a low capacity” (i.e., physiological grade).
Wakeley (1954) [11]	Recognized importance of physiological quality for survival and growth. Seedlings within a defined height range and increasing stem diameter grew best.
Stone (1955) [13]	“If the root system did not increase in size at a fairly rapid rate ... the seedlings would die of drought ... ”
Stone and Schubert (1959) [14]; Stone et al. (1962) [15]	Determined that periodicity of root regeneration potential was the basis for defining lifting and cold-storage schedules that avoided early plantation failures.
Rowe (1964) [16]	Proposed that preconditioning might be useful for acclimatizing seedlings to improve their field performance.
Lavender and Cleary (1974) [17]	“ ... seedlings must be produced in such a way as to be physiologically ready to outplant into the field environment”
Tinus (1974) [18]	Seedlings must be in the “proper physiological state” to survive in the field environment.
Lavender (1976) [19]	Recognized importance of seedling physiology for field performance; initial stages of articulating seedling quality.
van den Driessche (1976) [20]	Stated “physiological factors likely to influence survival and growth,” but questioned whether they can be incorporated into “a grading system”
Cleary et al. (1978) [21]	Seedlings with appropriate morphological characteristics that are properly conditioned and vigorous positively “influence(s) reforestation success”
Sutton (1979) [22]	Morphological attributes related to seedling performance, but variability in field performance leads to conclusion it is “ ... not what a tree looks like but how it performs in the field”
Sutton (1980a) [23]	“The quality of planting stock is the degree to which that stock realises the objectives of management at minimum cost. Quality is fitness for purpose.”
Sutton (1980b) [24]	“In stressful outplanting situations ... morphology is an inadequate or misleading indicator of performance.”
Timmis (1980) [25]	Physiological variables define seedling performance; seedling response to site conditions drives growth.
Chavasse (1980) [26]	Seedling appearance is not a good measure of field performance. All steps in regeneration silviculture affect field performance.
Schmidt-Vogt (1981) [27]	Stress tolerance of seedlings “holds a key position” in the establishment of forests.
Burdett (1983) [4]	First comprehensive list of seedling characteristics that “enhance early plantation performance”
Iverson (1984) [28]	The biological goal is to plant seedlings that have the desired genetic, morphological, and physiological characteristics to utilize site resources most fully.
Ritchie (1984) [29]	Morphological characteristics exert primary influence on performance when seedlings are physiologically sound.
Duryea (1985a) [30]	The first seedling quality compendium detailing application of many seedling attributes still commonly used in assessment programs.
Duryea (1985b) [31]	“Having a wide array of tests to choose from may soon enable us to predict a seedling’s suitability to a particular planting site ... ”
Kramer and Rose (1986) [32]	Physiological processes are the “machinery” through which genetics and nursery culture determine seedling quality.
Glerum (1988) [33]	Attributes define a seedling’s “performance potential”, but sound silvicultural practices are required for “optimal field performance”

Table 1. *Cont.*

Author(s)/Date	Relevance to the Discipline of Seedling Quality
Lavender (1988) [34]	"At present there is no really effective method to measure seedling vigour."
Puttonen (1989) [35]	Morphological traits describe "overall suitability" and physiological traits predict "acclimatization" to the site.
Hawkins and Binder (1990) [36]	"...no one test will be able to predict stock quality...," rather an integration of tests is required to define "seedling fitness" for field performance.
Rose et al. (1990) [37]	The "target seedling concept" was developed to define specific morphological and physiological seedling attributes "that can be quantitatively linked to reforestation success"
Johnson and Cline (1991) [38]	No single test is best and a "battery of tests is required to consistently predict seedling quality"
Langerud (1991) [39]	The term "viability" is the best descriptor for tests assessing seedling quality.
Omi (1993) [40]	No single attribute can "solely predict outplanting success". However, a "wide array of seedling tests may be impractical"
Grossnickle and Folk (1993) [41]	A combination of tests simulating field conditions are required to forecast, not predict, growth.
Folk and Grossnickle (1997) [42]	The distinction between seedling quality testing for initial survival or growth potential is required for better decision making in forest restoration programs.
Mattsson (1997) [43]	Single morphological attributes cannot forecast performance. A combination of morphological and physiological attributes can possibly "predict field performance"
Mohammed (1997) [44]	Measurement of attributes is critical for defining viable seedlings that can survive in the field, although it is difficult to reliably forecast growth.
Puttonen (1997) [45]	Morphological attributes can be used to "predict field performance"
Grossnickle (2000) [2]	Attributes supply useful performance information, although there are forecasting limitations depending on timing of tests and field site conditions.
Colombo (2004) [46]; Wilson and Jacobs (2006) [47]	First reviews to focus on hardwoods; their unique characteristics mean alternative morphological attributes or timing of physiological measurements should be considered.
Haase (2008) [48]	Many morphological and physiological variables can be measured to track and assess seedling quality. Defined a list of most commonly used morphological and physiological measurements of forest seedlings.
Ritchie et al. (2010) [49]	Morphological attributes "seldom change" after lifting, thus they project to the field, whereas physiological attributes "provide only a momentary analysis of plant quality"
Villar-Salvador et al. (2010) [50]	Review focused on the uniqueness of Mediterranean woody species and that, although somewhat similar, seedling quality practices need modification for species of this geographic region.
Landis (2011) [51]	The "target seedling concept" expanded to the "target plant concept" thereby including all types of plant materials (e.g., trees, shrubs, grasses) and including seeds, cuttings, or wildlings, as well as traditional nursery stock.
Dumroese et al. (2016) [52]	Application of the "target plant concept" to the nursery manager-client partnership with the goal of meeting forest restoration objectives.

In the mid-20th century, researchers began to critically examine what it took to grow quality seedlings in nurseries and what plant attributes conferred improved field performance (Table 1). These programs initially focused on bareroot seedlings [10,11,13]. Many of these measurements were related to morphological attributes [11] or root growth [13]. However, physiological attributes [10] and periodicity of root growth [14,15] were recognized as important factors affecting field performance.

In the 1970s, the emergence of container nurseries with their inherent ability to have greater control of cultural practices [53] created a realization that seedling physiology could be manipulated to change seedling quality (e.g., [17,18,54]). This realization began with the idea, proposed by Rowe [16], that cultural practices could be applied to acclimatize seedlings and improve their field performance. At this time, selection of species and locally adapted genetic sources also became part of the seedling quality discussion [18]. Together, these changes gave researchers and practitioners an opportunity to produce quality container-grown seedlings that resulted in new standards of field performance [55]. This was the start of seedling quality programs based on the need for a better understanding of seedling performance capabilities in relation to forest restoration sites (Table 1).

In the late 1970s and early 1980s, forest scientists were discussing the morphological and physiological attributes of seedling quality (Table 1). At this time, Sutton [23] proposed defining seedling quality as "fitness for purpose", meaning that seedlings are grown not just for the sake of producing nursery stock, but rather to achieve some objective(s) of management [24]. Subsequently, it became the standard definition for seedling quality, and remains so to this day [49,52]. Interestingly, this definition also mirrors one of the basic tenets of quality-assurance programs in manufacturing, i.e., that the product should be "fit for purpose" [56] (see Section 3.1).

Sutton [24] suggested that improvements in seedling quality would only occur when both morphological and physiological attributes were considered. Jaramillo [57] was one the first to provide a brief list of measurement techniques to evaluate seedling quality. Burdett [4] proposed a more comprehensive list of morphological (e.g., bud, shoot, root) and physiological (e.g., carbohydrate reserves, dormancy, drought tolerance, freezing tolerance, nutrient status) attributes which, if present in seedlings within the proper range of values, would "enhance" seedling performance after planting. These measured attributes quantify a seedling's growth potential, with field performance dictated by how site conditions affect this potential [58]. Burdett [4] proposed that phenotypic traits created during nursery culture were necessary for matching seedlings to site conditions (i.e., that these traits "preadapted" seedlings). Furthermore, he considered these phenotypic traits to be just as important as genotypic traits in determining initial field performance [4].

Further refinement of what seedling attributes defined field performance occurred during the early to mid-1980s (Table 1). Ritchie [29] articulated seedling properties that describe material attributes (i.e., single measures of seedling parameters) and performance attributes (i.e., integrated measures of various material attributes to test conditions). Iverson [28] believed that seedling selection needed to be based on that genetic, morphological, and physiological attributes that would be best suited to the intended field site. Duryea [31] envisioned that choosing from a wide array of attributes would allow one " ... to predict a seedling's suitability for a particular planting site ... ", thereby ensuring successful forest establishment. Furthermore, she believed a testing approach defining seedling quality just before planting would be desirable [31]. Moreover, Navratil et al. [59] voiced the need for an integrated stock quality program that assessed seedlings through all facets of the forest restoration process to improve both nursery production and restoration success.

Between 1988 and 1999, various researchers concluded that seedling quality could not be determined by an individual morphological or physiological attribute in isolation from other attributes (Table 1). In addition, it was recognized that measured attributes had to define seedling growth in relation to anticipated site conditions [35,36,60]. At this time, the "target seedling concept" was proposed, which suggested that "numerous seedling traits must work together to produce the desired field response" [37] (see Section 3.1). However, Langerud [39] warned that any measured attribute is a just a point-in-time assessment. Furthermore, a performance potential index was proposed at this time [61]. The idea was to create a battery of measured attributes that defined seedling performance in relation to potential field conditions [41]. Simpson and Ritchie [62] felt that the ability of a measured attribute (i.e., root growth potential) to define field performance was a function of both the seedling's level of stress resistance and the field site conditions. It was suggested that if the desire was to come closer to forecasting seedling field performance, then testing conditions should simulate environmental conditions at the planting site [42].

The range of seedling quality testing approaches continued to expand through the 1990s [2,43,44], even though many practitioners desired a single test that could measure seedling quality (Table 1). In a provocative paper, Puttonen [45] addressed whether there was the single "silver bullet" test that could be used in seedling quality assessment programs. He suggested that grouping morphological attributes together showed the best evidence of having "predictive value" in defining field performance, because they retain their mark on seedling identity for an extended time after the seedlings are field-planted and start to grow. Thus, such a grouping was the best candidate to be the "silver bullet" test [45]. However, Puttonen [45] concluded that physiological status cannot be ignored. This was in agreement with what other researchers were stating: that individual quality assessments should not be done in isolation [34], and that a combination of morphological and physiological attributes are required to describe seedling quality (e.g., [41,43]).

As the field of seedling quality expanded to hardwoods, it was recognized that, although some conifer attributes were applicable to hardwoods, these genera had unique attributes when it came to quality assessment procedures (Table 1). Variation in hardwood phenology and ecology requires that sampling periods and sampled tissues need to be carefully considered when devising a quality assessment program [47]. Species-specific variation also creates a need to modify quality-assessment approaches [50]. Thus, refinement of conifer procedures was needed to effectively measure the quality of hardwood seedlings.

In conclusion, from the realization that establishment success was associated with seedling attributes [5], through recognizing that seedling attributes were related to seedling performance [11], to defining these measurements as being related to a seedling's "fitness for purpose" [23], these perspectives have focused on defining seedling attributes that define their field performance. Moreover, this view was the main premise of the "target seedling concept" [37]. Use of this concept within an operational setting [63] was viewed as an effective way to create a nursery–client partnership that would permit open dialogue leading to a successful restoration outcome [51,64–66]. Finally, the idea that this concept be expanded to include native plant (i.e., woody and non-woody forest and range species) material (e.g., seedlings, cuttings) used in restoration programs has been proposed, and is known as the "target plant concept" [51,52,64,66].

3. Application of Seedling Quality within a Forest Restoration Program

Seedling quality assessment procedures occur in the nursery both during culture (see Section 3.1) and at lifting (see Section 3.2). The following is a review of the conceptual approach used to assess seedling quality from these two perspectives.

3.1. Monitoring the Process

In Monitoring the Process, the nursery manager creates a system for monitoring culture practices and crop development, which allows them to grow seedlings to the desired specifications. The proper application of nursery practices to produce quality seedlings is a key component of successful restoration programs using both bareroot [67,68] and container-grown [2,55,69] seedlings. To develop an effective seedling quality program that monitors the process, one needs to understand how the crop responds to cultural conditions. A crop's physiological response to the environment and its subsequent developmental response ultimately determine its growth performance in the nursery [70]. If nursery staff understand a species' physiological capability in relation to environmental conditions, then these detailed cultural practices can become standard operating procedures (SOPs). Various authors have suggested that SOPs need to be integrated into crop plans to consistently produce high-quality seedlings each year, whether they are bareroot [11,67,71] or container grown [55,72].

A conceptual model for monitoring a nursery production system that consistently produces high-quality seedlings is outlined in Figure 1. As mentioned, to create SOPs, one needs to fully understand each species' performance attributes, which entails understanding the ecophysiological and growth characteristics that define seedling development. Furthermore, SOPs for a given species can vary significantly with seedlot and/or target morphological and physiological specifications needed for a given outplanting site. In addition, SOPs for every phase of nursery culture need to be created because seedling development changes throughout culture. Furthermore, SOPs are the 'knowledge tools' nursery practitioners develop and subsequently use to guide them through each crop production cycle.

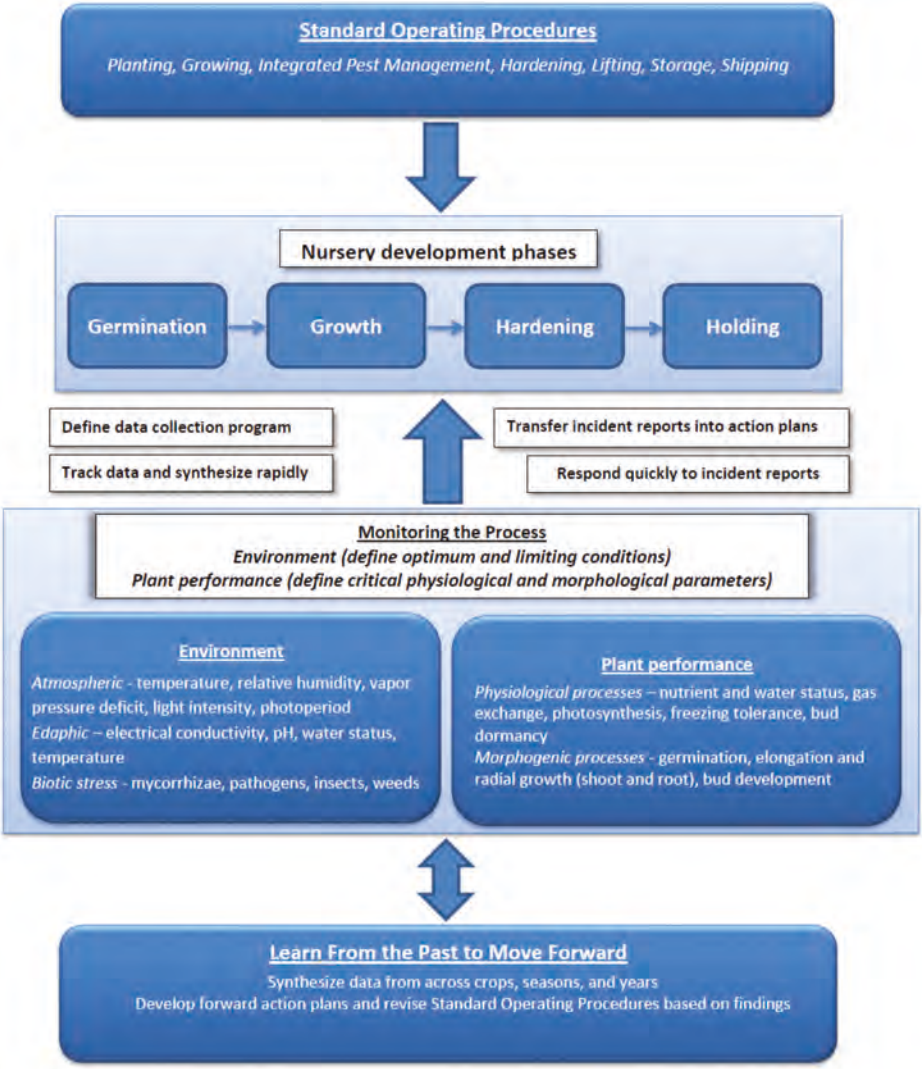

Figure 1. Conceptual model for monitoring seedling quality during crop development in the nursery.

Once the crop plan with SOPs has been developed, a tracking system is needed to ensure cultural guidelines are being followed and the crop is growing according to the plan (Figure 1). Such a system involves tracking both the nursery environment and crop performance [73]. Environmental conditions are tracked to define both optimum and limiting conditions for crop performance. Atmospheric conditions (e.g., air and plant temperature, relative humidity or vapor pressure deficit, light intensity, carbon dioxide level) and edaphic parameters (e.g., substrate temperature, substrate water content) can be monitored continuously with automated environmental sensors. Fertigation parameters (e.g., pH, electrical conductivity) can be monitored by handheld devices or semipermanent substrate probes. Automation of environmental monitoring provides rapid data synthesis that allows one to quickly understand how various parameters are affecting crop performance.

Crop performance is tracked by selecting morphological and physiological parameters that both mark important stages in seedling development [39] and can be easily measured. Alternatively, new technologies (e.g., fluorescence-imaging systems [74]) are becoming available that measure crop performance at a large scale and provide staff with the ability to understand how cultural practices are affecting seedling ecophysiological response. Such technology can be integrated with the irrigation system so that irrigation/fertigation automatically occurs at the first sign of stress. However, one also needs to "walk the crop" on a regular basis, thereby ensuring that the measured data corresponds with actual crop development. Furthermore, continued monitoring of the crop for pests is a critical part of maintaining crop quality during nursery development.

A crop performance database, together with a database for operational and cultural adjustments to the crop plan, is needed for such a monitoring system. Data collection and entry need to be efficient, as ongoing data analysis alerts staff when an incident that takes the crop away from the intended plan has occurred. In addition, one needs to understand seedling development in relation to planned cultural practices and use assessments to discern if corrective actions are needed to ensure the development of quality seedlings. Then, remedial action can quickly be taken to return to the crop plan. Deviations from the crop plan are recorded, so that after crop lifting, a crop review allows nursery staff to develop an understanding of what worked, what didn't, and where improvements in the crop plan can be made (Figure 1). In addition, deviations are compared with crops across a number of years to gain a perspective on crop performance under a range of conditions. Both retrospections allow the nursery practitioner to make adjustments to cultural practices, thereby further refining SOPs to improve future crop performance. In this way, a quality assurance program develops, and becomes a system of positive change and continued improvement in crop cultural practices.

This approach is part of the "target seedling concept", in which attention to the crop plan, as proposed above, is important to achieving the desired seedling product [37,75]. This approach is also similar to ISO quality assurance programs that monitor the production process to ensure achievement of planned results [56,76]. Furthermore, Grossnickle [73] described a quality-assurance program designed and operated at ten nurseries across North America that produced tens of millions of high-quality somatic loblolly pine (*Pinus taeda* L.) seedlings, which were planted throughout the southeastern United States. Creating and running this quality program demonstrated that, when designed to monitor the process, quality seedlings were the final output [73].

3.2. Monitoring the Product

In Monitoring the Product, an information database is created that allows dialogue between nursery and client on seedling performance capabilities. When nursery staff and silviculturists consider using a quality-assurance program to assess their seedlings, two questions are commonly asked. How to select stock that ensures the best field performance after planting? How to select tests that are useful in culling seedlings that do not meet desired quality standards? These questions are addressed in the paragraphs below.

A conceptual model for modeling seedling quality at the end of nursery practice is presented in Figure 2. This model provides a perspective on how one applies various assessment procedures when measuring seedling attributes that define field survival and/or field growth potential. Ritchie [29] discussed seedling quality in terms of material and performance attributes. Material attributes are single-point measures of individual parameters representing specific plant subsystems (e.g., morphology, osmotic potential, root electrolyte leakage, nutrient content/concentration, individual gas exchange measurements). In contrast, performance attributes reflect an integration of various material attributes, are environmentally sensitive plant properties, and are measured under specific testing conditions (e.g., root growth potential, freezing tolerance, 14-day gas exchange integrals). Both attribute types provide information on initial survival and field performance potential. Nursery staff and silviculturists need to define specific objectives before selecting testing procedures within a seedling quality program. In this way, they will achieve one of the basic principles of the "target seedling concept", which is for nurseries to deliver seedlings with morphological and physiological attributes that meet targets set by land managers for their restoration program [37,52] (see Section 2).

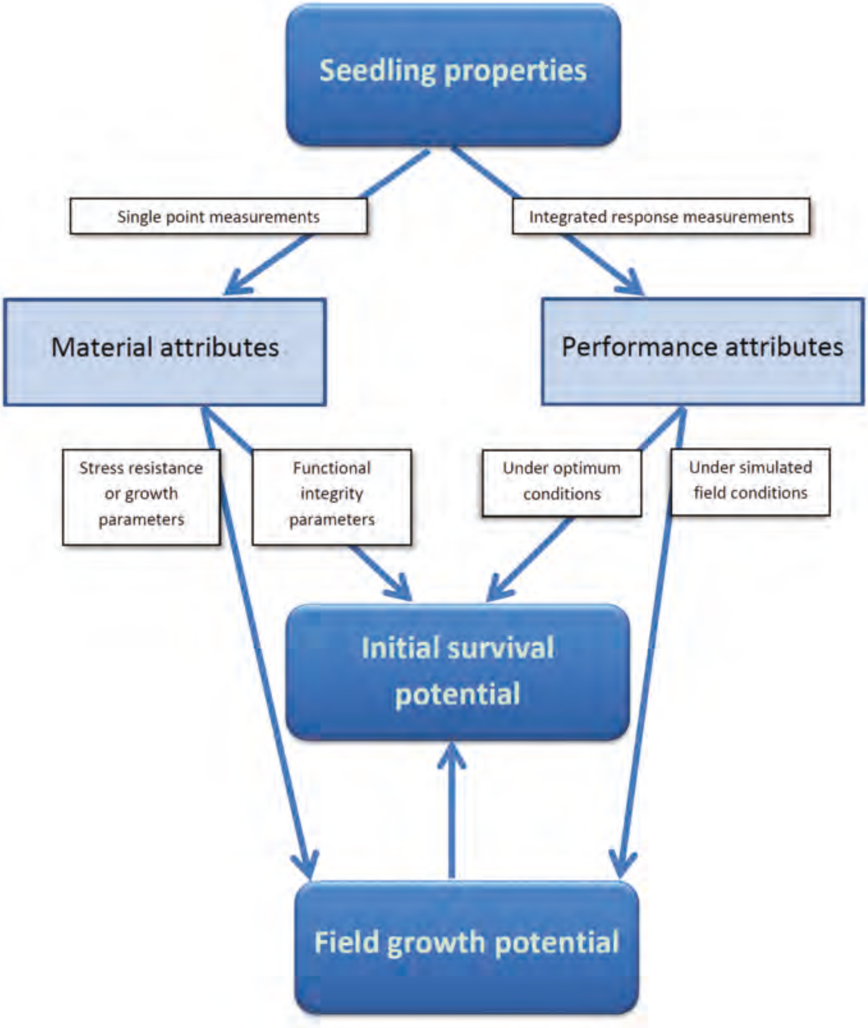

Figure 2. Conceptual model for monitoring seedling quality at the end of nursery culture (adapted from Folk and Grossnickle [42]).

One can never assume that planting high-quality seedlings "predicts" good field performance, as success is also influenced by appropriate silvicultural treatments before planting, as well as site conditions after planting [39,41,77]. After seedlings are planted, they may undergo various transplanting stresses before they can initiate growth and become "coupled" with the forest ecosystem [78]). Furthermore, if these environmental stresses are excessive [78], or seedlings have "too low a viability for the planting site" [39], then mortality [79] or a lack of proper growth [80] can occur. This is why seedling growth just after planting is critical to seedling survival and establishment [81,82]. Furthermore, once seedlings are established, seedling performance depends on inherent growth potential (which is related to their morphological and physiological attributes), together with their ecophysiological response to site environmental conditions that limit or enhance that potential [2]. The degree to which seedlings are suited to site conditions has the greatest influence on their performance immediately after planting [4,37]. Finally, as part of a comprehensive forest restoration program, measurement of seedling quality provides the silviculturist with information to "forecast" future plantation performance.

In planning a seedling quality program, one needs to choose attributes that assess seedling potential both to survive initially and to grow after field planting. The following paragraphs discuss attributes that measure initial survival potential and growth potential.

Initial survival potential is a measure of seedling "functional integrity" [41]. Functional integrity indicates whether seedlings are, or are not, damaged to the point of limiting primary physiological processes. Indeed, seedlings with reduced functional integrity can have poor field survival [2,79]. That said, seedlings meeting minimum standards typically have the capability of surviving in all but the most severe field site conditions [60]. Testing for functional integrity can be used at lifting to cull seedlings that do not meet minimum physiological performance standards, and includes assessment techniques such as root growth potential, root electrolyte leakage, and chlorophyll fluorescence. Root growth potential [13,62,83–87] and root electrolyte leakage [88,89] indicate root system integrity. Shoot system integrity is indicated directly by chlorophyll fluorescence [90–92] and indirectly by root growth potential [29]. Morphological attributes such as shoot height, stem diameter, root mass, and shoot-to-root ratio, together with physiological attributes such as drought resistance, mineral nutrient status, freezing tolerance, and root growth, have been shown, in some instances, to forecast survival after planting (reviewed by [2,79]). However, there is no guarantee that testing for initial survival potential provides information on field growth under limiting environmental conditions.

Plant attributes forecasting field growth need to define the intrinsic growth potential of seedlings with regard to site conditions [60]. A number of plant attributes measured at lifting (e.g., height, diameter, shoot-to-root ratio, root growth potential, nutrient status, drought resistance, freezing tolerance) have been reviewed for their capability to forecast growth [80]. When considering a more detailed assessment of seedling performance potential, it is important to select plant attributes that characterize performance in relation to the anticipated field site environmental conditions [31,35,36,41,42,60] (Figure 2). However, field conditions can only be roughly simulated. Furthermore, these are single-point assessments within a seasonal performance pattern [41] that changes as seedlings go through their phenological cycle [70]. Therefore, this approach forecasts, but is not able to predict, field performance. With these caveats in mind, multiple plant attributes have been combined that characterize seedling performance relative to stress events typically encountered on restoration sites (e.g., performance potential index [61], covariate morphological attributes [93], multivariate analysis [94], multiple variable models [95]) and provide forecasting models.

4. Plant Attributes that Define Seedling Quality

Plant attributes have been assessed at the morphological and physiological levels (Tables 2 and 3). However, in reality, only a limited number of these attributes are used within operational programs [44], because an "ideal operational measure" needs to be rapid, simple, cheap, reliable, nondestructive, quantitative, and diagnostic [96]. Indeed, researchers have agreed that only a subset of the most easily measured attributes listed in Tables 2 and 3 [48–50,97] be considered for seedling quality programs in nurseries [2,4,36,41,43–45]. However, each researcher has his/her preferred attributes. Furthermore, the "ideal operational measure" filter has also limited the operational use of comprehensive tests that combine multiple morphological and physiological attributes [36,43,45,97].

Table 2. Morphological attributes commonly used in seedling quality assessment programs to monitor either the process during nursery culture or the product at the end of culture.

Attribute	Application	Monitor the Process	Monitor the Product	References [1]
Bud development	Growth		×	[98–100]
Dry weight fraction	Lift/store	×		[101–103]
Height and diameter	Crop development	×		[11,21,37,55,75,104]
Height and diameter	Survival, growth		×	[4,5,11,21,22,26,27,29,104,105]
Morphological ratios	Survival, growth		×	[4,5,11,25,29,35,98]
Root system	Crop development	×		[11,21,37,75,104,106]
Root system	Survival, growth		×	[4,5,11,19,27,32,33,35,98]
Shoot and root weight	Survival, growth		×	[11,98]
Shoot system dimensions	Growth		×	[2,107]
Qualitative shoot trait [2]	Survival, growth		×	[5,11,48–50,98]
Qualitative root trait [3]	Survival, growth		×	[5,11,48–50,97,98]

[1] References are either the initial research conducted on an attribute and/or citations that initially recognized the attribute for inclusion in seedling quality programs at nurseries; [2] Examples: lack of terminal bud, multiple stems, stem curvature; [3] Examples: deformed root, poor plug development.

Table 3. Physiological attributes commonly used in seedling quality assessment programs to monitor either the process during nursery culture or the product at the end of culture.

Attribute	Application	Monitor the Process	Monitor the Product	References [1]
Chlorophyll fluorescence	Lift/store, viability	×		[90–92,108,109]
Chlorophyll fluorescence	Survival, growth		×	[48,49,110]
Freezing tolerance	Lift/store	×		[25,29,33,35,111,112]
Freezing tolerance	Survival, growth		×	[29,33,35]
Nutrient status	Crop development	×		[11,17,21,55,67,71,113–115]
Nutrient status	Survival, growth		×	[4,11,18,35,116–119]
Pest status	Crop development	×		[38,55,120–122]
Pest status	Survival, growth		×	[11,97]
Plant water status	Crop development	×		[21,115,123]
Plant water status	Survival, growth		×	[38,124–126]
Root electrolyte leakage	Crop development	×		[49,127]
Root electrolyte leakage	Survival, growth		×	[49,88,89,126]
Root growth potential	Survival, growth		×	[4,13,21,29,33,35,83–87]

[1] References are either the initial research conducted on an attribute and/or citations that initially recognized the attribute for inclusion in seedling quality programs at nurseries.

Despite these challenges, assessment programs for nurseries have been developed by selecting a set of attributes whose intended purpose is to ensure quality control, enhance consumer confidence, avoid planting damaged stock, and improve nursery cultural practices [50,97,128–130]. In addition, there have been a number of published discussions describing measurement procedures for the most common attributes (e.g., [48,49,97]). As mentioned, the field of seedling quality has evolved to the point that nursery practitioners and silviculturists now have a range of plant attributes that they can measure to understand the quality of their seedlings. The following discussion briefly examines the application of commonly used morphological (Table 2) and physiological (Table 3) attributes in forest restoration programs.

4.1. Commonly Used Plant Attributes

Morphological and physiological attributes are used to measure crop development in the nursery (See Section 3.1). Commonly measured morphological attributes include height, diameter, and root development for bareroot (e.g., [11,104]) and container-grown (e.g., [55,75]) seedlings. Typically, height and diameter are compared with standardized growth curves defined for each species, seedlot, and stocktype, which allows the adjustment of the nursery environment and cultural practices in order to keep seedlings on the crop plan. Root development is also monitored in container-grown seedlings to determine plug integrity, which is critical at lifting [131]. Physiological attributes commonly measured during crop development include nutrient status and plant water status. These attributes provide information for tracking crop performance, thereby supporting cultural adjustments to the crop plan. However, root electrolyte leakage is measured during crop development if there is a concern about damage. Furthermore, measuring chlorophyll fluorescence, electrolyte leakage, or whole-plant freezing during crop development in the autumn provides an assessment of freezing tolerance, with the goal of determining the proper lift/store date to develop sufficient stress resistance so high quality seedlings are stored (reviewed by [109,132,133]). Finally, at lifting, various morphological attributes, together with the physiological attributes of plant water relations, freezing tolerance, mineral nutrient status, root growth potential, and root electrolyte leakage are commonly assessed (See Section 3.2).

Morphological attributes are also used to relate seedling quality at lifting to subsequent field performance (See Section 3.2). Commonly measured morphological attributes include height, stem diameter, root systems, and shoot-to-root ratios [134]. These attributes are easy to measure in operational settings, ensuring their use in small-scale nurseries in developing countries [135] and large, commercial nurseries in first-world countries [2,136,137]. Morphological attributes influence seedling survival and growth after planting on forest restoration sites, because they retain their mark on seedling attributes for extended timeframes (reviewed by [79,80]). Greater stem diameter and root system size confer a higher chance of survival and growth, because they limit susceptibility to planting stress by improving water uptake and transport to foliage. Interestingly, South [138] revisited the morphological criteria defined by Wakeley [11] and found that root collar diameter was still the attribute that best forecast field growth potential. Greater height provides a competitive advantage (i.e., access to light) on sites with competing vegetation. However, where potential site environmental conditions are limiting (e.g., dry soils, high evaporative demand), seedlings with smaller shoot systems or lower shoot-to-root ratios are better adapted. Finally, morphological attributes are only measures that help define overall seedling size, growth potential, and balance [98,105], whereas seedling physiological attributes also have a major influence on field performance.

Other morphological attributes have been used in seedling quality programs, but with limited acceptance (Table 2). Bud development has been used in Ontario, Canada as a measure of potential seedling shoot growth [97]. Dry weight fraction has been used in Scandinavia to assess the development of stress resistance in the fall (c.f. [102]). Shoot dimensions (i.e., phyllotaxy of needles on shoots and arrangement of shoots along the leading stem) can be an important measure of seedling development for some (e.g., spruce [139]) but not all species.

Physiological attributes are also used to relate seedling quality at lifting to field performance after planting (See Section 3.2). Drought resistance, mineral nutrient status, root growth potential, root electrolyte leakage, and freezing tolerance have been used to assess seedling quality in relation to field survival (reviewed by [79]) and growth (reviewed by [80]) after planting. Improved survival is to the result of greater drought resistance and improved seedling nutrition at planting, which increases the speed with which seedlings can overcome planting stress, become established, and grow on the forest restoration site. Shoot water potential and root electrolyte leakage provide critical information on whether seedlings are damaged to the point of limiting physiological function; planting undamaged seedlings improves their survival and growth. Additional measurement of seedling functional integrity (e.g., root growth potential) is recommended if earlier tests detect a level of damage that could potentially limit field performance. Root growth potential on its own is valuable in many instances in forecasting field performance, because improved survival and growth due to greater root growth immediately after planting (reviewed by [79,80]) confers improved seedling survival and subsequent establishment within the first few months after planting.

In conclusion, it is important to emphasize that no single attribute can assess all seedling quality issues [43,45]. Morphological attributes cannot be used in isolation to assess seedling quality because morphology does not describe physiological vigor [105,134]). Furthermore, seedling quality cannot be determined by individual physiological attributes in isolation from other physiological and morphological attributes [34]. Thus, a seedling quality program needs to combine morphological and physiological attributes to provide the information necessary for making both sound nursery cultural decisions and restoration site decisions. Furthermore, a combination of desirable morphological and physiological attributes forecasts greater chances of survival and increased growth after establishment.

4.2. Novel Attributes and Tests for Plant Attributes

As the field of seedling quality assessment has developed, “novel” attributes and measurement techniques have been examined for their usefulness. The following paragraphs briefly outline novel physiological attributes or novel measurement techniques for traditional physiological attributes (Table 4), and novel biochemical, biophysical, and molecular techniques (Table 5).

Table 4. Novel physiological attributes or novel measurement techniques for traditional physiological attributes, proposed for use in seedling quality-assessment programs to monitor either the process during nursery culture or the product at the end of culture, which were not adopted.

Attribute or Technique	Application	Monitor the Process	Monitor the Product	References [1]
Auto-fluorescence	Viability		×	[44,140]
Bud dormancy	Lift/store, viability	×		[29,112,141,142]
Carbohydrate status	Survival, growth		×	[143–146]
Chlorophyll content, foliage color	Crop development	×		[147]
Chlorophyll content, foliage color	Growth		×	[24,49,98]
Crop-level chlorophyll fluorescence	Crop development	×		[74]
Drought avoidance	Survival, growth		×	[148]
Drought tolerance	Survival, growth		×	[4,11,19,25,27,29]
Electrical impedance	Lift/store, viability	×		[111,149,150]
Gas exchange [2]	Survival, growth		×	[107,151,152]
Heat tolerance	Survival		×	[153]
Infrared thermography	Lift/store, viability	×		[154–156]
Mycorrhizal status	Growth		×	[157–161]
Nuclear magnetic resonance	Survival		×	[162]
OSU [3] vigor test	Survival		×	[34,125,163]
Performance under stress	Growth		×	[42,61]
Root hydraulic conductivity	Survival, growth		×	[164–166]
Stress-induced volatile emissions	Survival		×	[167–170]
Xylem cavitation	Survival		×	[171–173]

[1] References are the initial work conducted on an attribute or a measurement technique; [2] Examples: needle conductance, photosynthesis, transpiration; [3] Oregon State University.

Table 5. Novel measurement techniques at the biochemical, biophysical, and molecular levels, proposed for use in seedling quality-assessment programs to monitor either the process during nursery culture or the product at the end of culture, which were not adopted or were recently reported in the literature.

Technique	Application	Monitor the Process	Monitor the Product	References [1]
Biochemical				
Enzymatic activity	Survival		×	[35,174]
Fluorescein diacetate staining	Viability		×	[175,176]
Triphenyl tetrazolium chloride staining	Survival		×	[36,177]
Vegetative storage proteins	Lift/store, viability	×		[103]
Biophysical				
Extracellular electropotential	Viability	×		[178–180]
Root electrical impedance	Lift/store	×		[181]
Molecular				
Gene expression	Lift/store	×		[182–186]
Molecular markers	Survival, growth		×	[187]

[1] References are the initial research conducted on a measurement technique in the context of seedling quality.

Some physiological attributes and measurement techniques were categorized as "novel" (Table 4), because other than in the articles describing them or in subsequent review articles, there is scant information that nursery practitioners are operationally using them. Indeed, when these attributes and techniques were compared against the criteria for "ideal operational measures" of seedling quality [96], many failed for one reason or another. Some fail the criterion of being rapid (e.g., bud dormancy, OSU vigor test). Others fail the criteria of simple and cheap because they require technically trained staff to run relatively expensive instruments for the analysis (e.g., drought tolerance, chlorophyll content, electrical impedance, infrared thermography, gas exchange, crop-level chlorophyll fluorescence, nuclear magnetic resonance, root hydraulic conductivity, stress-induced volatile emissions, xylem cavitation). Furthermore, whether the information is a reliable assessment of seedling quality (e.g., drought avoidance, foliage color, mycorrhizal status) plays a role in whether a nursery would spend the time to conduct the test.

Most of the biochemical, biophysical, and molecular techniques (Table 5), which were developed during the late 1980s and early 1990s have yet to be applied in nurseries. In general, molecular testing has not fulfilled the expectation voiced over 20 years ago that they would offer rapid measures of seedling quality [45]. However, more recent gene-expression analysis on freezing tolerance [188] has the potential to replace other tests (e.g., whole-plant freezing, electrolyte leakage, chlorophyll fluorescence [109,111]) used to make lift/store decisions. Genes involved in freezing tolerance in Scot's pine [188], Norway spruce [188], and Douglas-fir [183] have been identified, and then correlated with results from shoot electrolyte leakage tests to develop an assay that measures gene activity during freezing tolerance acquisition [188]. Furthermore, a related spin-off company (nsure®) has commercialized the assay. Clients sample, stabilize, and ship shoot tips to the lab, which conducts the test; level of freezing tolerance is e-mailed to clients within 2 days of sample arrival at the lab. It is yet to be determined whether this assay will replace the traditional measures of freezing tolerance used by nurseries.

5. Summary

Seedling quality is an important component of any successful forest restoration program. Over the past century, the concept of what is meant by seedling quality has evolved to the point that these plant attributes are used to improve seedling nursery culture and to forecast seedling survival and growth after outplanting. Such seedling quality information can now be used within the "target forest or plant seedling" concept to enable nursery practitioners and foresters to have an effective dialogue on how seedlings with certain attributes will meet forest restoration objectives. Even though planting seedlings with desirable plant attributes does not guarantee high survival and good growth after planting, planting seedlings with desirable attributes increases chances for a successful forest restoration program.

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