Recent Trends in Hardwood Seedling Quality Assessment

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Abstract: The study and evaluation of hardwood seedling quality has been attracting more attention in recent years. This is in contrast to the many decades of extensive research on conifer seedling quality. As demand and production of hardwood seedlings increase, a need arises for efficient, replicable, and practical approaches to quality assessment. Many methods of determining conifer seedling quality may be transferred to hardwood production systems. However, the genetic, morphological, and physiological characteristics of hardwoods merit special consideration when applying these concepts. Current techniques for evaluating seedling quality are discussed.

Keywords: morphology, physiology, genetics, hardwood production, hardiness, dormancy

Introduction

Seedling quality is a term used to describe the extent to which a seedling may be expected to successfully survive and grow after outplanting (Duryea 1985; Mattsson 1996). While this is heavily dependent on factors such as species, nursery culture, storage, site conditions, and genetics, a quality seedling can be defined as one that will thrive once outplanted in the field. For many decades, measurement of morphological and physiological characteristics has been used as a tool to predict field performance of seedlings. Research into cultural treatments and procedures that result in optimal levels of these parameters has been of prime importance, as has the evaluation of different methods of assessment.

Because conifers dominate nursery production in all parts of the world, researchers have focused primarily on issues regarding their production and establishment. In the US alone, conifers represent 80 to 90% of total annual seedling production (1.7 billion trees) (Moulton and Hernandez 2000). Conifer species such as white pine (*Pinus strobus* L.), loblolly pine (*P. taeda* L.), red pine (*P. resinosa* Ait.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and white spruce (*Picea glauca* (Moench) Voss) have a long history of quality grading and nursery production research (Ziegler 1914; Wakeley 1948; Curtis 1955; Stone 1955; Slocum and Maki 1956; Dickson and others 1960). This review summarizes some of the more common methods of assessing seedling quality through morphological and physiological characteristics.

Increasing Importance of Hardwoods

As hardwood seedling demand has increased, identifying effective means of assessing quality has become more important. An example of this growing demand may be seen in the Central Hardwood Region. In recent years, the 12 northeastern and midwestern states that comprise this region have been experiencing a severe shortage of hardwood seedlings. In 1999, it was estimated that demand outpaced supply by 25 to 50 million seedlings (Michler and Woeste 1999), with that demand expected to rise 20% annually. Rather than timber production, a major reason for this trend is concern over conserving soil and water resources and an interest in improving wildlife habitat through greater biodiversity, as evidenced by bottomland hardwood reforestation in the Lower Mississippi Alluvial Valley (King and Keeland 1999). Private landowners who outplant hardwoods are also interested in leaving a legacy for future generations (Ross-Davis and others forthcoming). The increase in hardwood production has prompted renewed interest in research programs and cooperatives that seek to advance regeneration and establishment practices. One such program is the Hardwood Tree Improvement and Regeneration Center (HTIRC). The HTIRC is a regional collaborative partnership between federal, state, university, and industry groups designed to expand basic and applied information about hardwood species. Programs such as these will concentrate on improving morphological, physiological, and genetic quality of hardwoods.

Hardwood and Conifer Differences

There are differences between conifers and hardwoods that affect approaches to quality assessment. Most conifers commonly used in forestry applications in the US belong to the Pinaceae family. Common hardwood species, on the other hand, are members of a number of different families: Aceraceae (*Acer*), Fagaceae (*Castanea* and *Quercus*), Hamamelidaceae (*Liquidambar*), Juglandaceae (*Carya* and *Juglans*), Magnoliaceae (*Liriodendron*), Oleaceae (*Fraxinus*), Platanaceae (*Platanus*), and Rosaceae (*Prunus*). Not only must one consider variation among species, but among families as well. Additionally, most hardwoods are broad leaved and deciduous, while most conifers have needlelike leaves and are evergreen. This can affect foliar analysis and diagnosis of problems associated with environmental stresses, particularly during the dormant months. Many hardwoods tend to exhibit more branching, have thicker roots, require higher fertility, and are more susceptible to pests and diseases when compared to conifers (Tinus 1978). All of these factors are important when developing appropriate protocols for evaluating hardwood seedling quality.

Another obstacle to overcome is lack of a substantial body of peer-reviewed scientific literature relative to that of conifers. There is need for rigorous statistical documentation of many issues related to hardwood regeneration. For instance, definitive guidelines describing optimal hardwood seedling morphological characteristics have not been published (Gardiner and others 2002).

Hardwood Seedling Quality

Morphological

Traditionally, seedling quality assessment of conifers has been conducted using morphological assessment. Morphological characteristics are easily and readily observed and measured (Ritchie 1984), making them more practical to use. Accordingly, morphology continues to be particularly useful for large scale grading. Many studies have evaluated variables such as height (Figure 1), stem diameter at root collar, root volume, fresh weight, bud size, and first order lateral roots (FOLR) for testing seedling quality of conifers (Kozlowski and others 1973; Reese and Sadreika 1979; Nambiar 1984; Rose and others 1991; Hallgren and others 1993; Ritchie and others 1993). Ratios of various morphological traits have also been considered (Bayley and Kietzka 1996). Not all of these variables are practical to implement on an operational scale; if superior predictors can be identified, it may be possible to modify cultural techniques to increase quality.

Hashizume and Han (1993) showed that the height of sawtooth oak (*Quercus acutissima* Carruth) seedlings was an important factor in determining growth and survival, with the tallest trees (>150 cm [59 in]) having lower survival percentages than trees 100 to 120 cm (39 to 47 in) in height. Thompson and Schultz (1995) found a negative correlation between initial height and first-year height growth of northern red oak (*Quercus rubra* L.), while the number of FOLR was positively and significantly correlated with height, diameter growth, and survival. In contrast, initial height of konara oak (*Quercus serrata* Thunb.) in Japan was positively associated with survival and weight after 5 years (Matsuda 1989).

Ruehle and Kormanik (1986) looked at FOLR as a possible indicator of northern red oak seedling quality. They found a significant correlation between the number of FOLR and height, as well as stem diameter and shoot and root mass. Kormanik and others (1995) mention positive correlations of FOLR with growth of northern red oak, white oak (*Quercus alba* L.), and sweetgum (*Liquidambar styraciflua* L.). Other studies have given mixed results about the usefulness of FOLR. Ponder (2000) showed positive correlations of FOLR with 4-year height growth of northern red oak and black oak (*Quercus velutina* Lam.) but no effect on growth of black walnut (*Juglans nigra* L.) and white oak. Data from Jacobs and Seifert (unpublished) indicated that FOLR was a poor predictor of height and diameter growth of northern red oak, white oak, and black cherry (*Prunus serotina* Ehrh.) after 1 year.

Figure 1—Measuring seedling height is a common method for morphological assessment.

Stem diameter, shoot length, and number of FOLR were correlated with second-year height and diameter of northern red oak 2 years after outplanting in Ontario, with initial stem diameter being the best predictor (Dey and Parker 1997). Stem diameter was also a good predictor of many root system traits such as volume, area, and dry mass. This is consistent with the results of Williams (1972) that showed that stem diameter was a better predictor of black walnut growth than root fibrosity. In the sweetgum research of Belanger and McAlpine (1975), the growth response of various root collar diameter grades was obvious after the first growing season and continued through the seventh season. At that point, trees from the largest seedling grade averaged 1.95 m (6.4 ft) taller than the trees from the smallest grade. Determination of various morphological ratios can also be an effective component of testing programs, providing an indication of balance between different plant parts. The root:shoot ratio is one of the most commonly used ratios. It is ratio of root mass to shoot mass and can often discriminate between high and low quality stock (Tomlinson and others 1996; Edwards 1998). This and other ratios, such as height:stem diameter, have not been extensively evaluated as potential quality indicators for hardwoods. Root volume, fresh weight, and bud size are among the many other traits that have been studied in conifers, but not to any significant extent with hardwoods.

Physiological

Differences in morphology often do not reflect variation in physiological condition. Morphological assessments of quality would have more validity if all the seedlings of interest were of the same physiological status. This may be the basis for much of the variation and inconsistency in past research (Ritchie 1984). Stone and Jenkinson (1971) found that ponderosa pine (*Pinus ponderosa* Douglas ex Lawson) seedlings of a high morphological grade might have a low root growing potential, even when outplanted into optimal growing conditions. If lifted and outplanted earlier or later, the same grade may have a high root growing potential. This result was best explained by differences in physiological status at time of outplanting. Because of results such as these, physiological quality testing has been gaining prominence. Physiological testing of conifers includes root growth potential (RGP), electrolyte leakage (EL), chlorophyll fluorescence (CF), water relations, nutrient status, enzymatic activity, and stress-induced volatile emissions (SIVE) (Landis 1985; McCreary and Duryea 1987; Orlander and Rosvall-Ahnebrink 1987; Lassheikki and others 1991; McKay 1992; Templeton and Colombo 1995; Mohammed and others 1997; Kooistra and Bakker 2002). These tests aim to quantify internal attributes such as stress resistance, dormancy status, and cold hardiness.

RGP testing (Figure 2) is by far the most common testing protocol (Simpson and Ritchie 1996). RGP is evaluated by placing seedlings in an optimal growing environment and assessing the initiation and elongation of new white roots (Sutton 1990). These tests can take weeks to complete, however. Rapid tests for estimating seedling physiological status are needed for nurseries to make timely management decisions on lifting, storing, and outplanting (Hawkins and Binder 1990). Recent research is evaluating these rapid methods. CF works on the concept that when plants are subjected to stress, changes in the photosynthetic pathways occur. Therefore, emission of light energy from the photosynthetic system varies according to the stress level. Using a chlorophyll fluorometer, this method is fast and nondestructive (Mohammed and others 1995). SIVE is a technique that has been the subject of recent research (Hawkins and DeYoe 1992; Templeton and Colombo 1995). It involves measurement of ethanol production from stressed seedlings. EL (Figure 3) has been used extensively for cold hardiness and dormancy status testing and is an indicator of cell membrane integrity and physiological activity. Mineral nutrition is important because it affects not only morphological characteristics such as height and root structure, but can indirectly affect indicators of physiological quality such as cold hardiness (Jozefek 1989). Tests of water potential and enzymatic activity are representative of the inherent stress resistance and viability of a seedling.

Figure 2—Evaluating root growth potential (RGP).

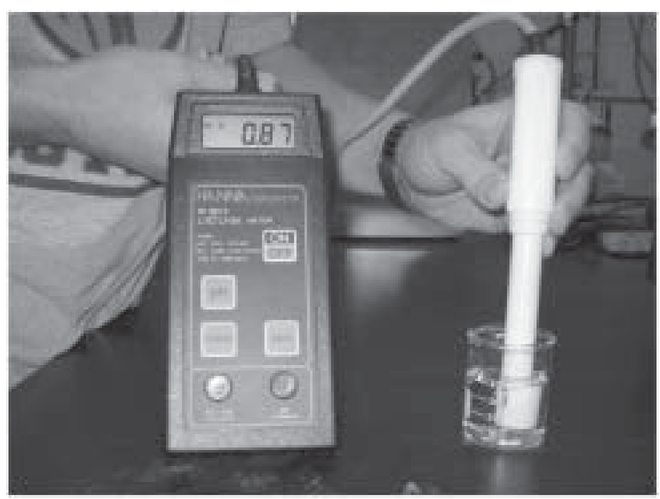

Figure 3—Electrolyte leakage (EL) from plant tissue samples.

Because of its potential in predicting field performance and improving establishment success in conifers, physiological quality testing has become operational practice in parts of the United States, Canada, Great Britain, and Sweden (Dunsworth 1996). There has also been an increase in research on physiological testing of hardwoods. O'Reilly and others (2002) employed an aerated hydroponics system to assess RGP of freshly lifted and cold stored ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.), where RGP was significantly correlated with height of freshly lifted ash after 1 growing season in the field. In the same experiment, shoot water potential (WP) and root electrolyte leakage (REL) were assessed for both species and storage regimes. WP was significantly correlated with height increment of cold stored sycamore; however, REL showed no significance for any variable. RGP has also been used successfully to predict field performance of European white birch (*Betula pendula* Roth.), English oak (*Quercus robur* L.) (Lindqvist 1998), and Holm oak (*Quercus ilex* L.) (Pardos and others 2003), with the highest RGP values related to increased growth and survival.

Stem WP was an effective predictor of field performance of European wild cherry (*Prunus avium* L.) and cherry plum (*Prunus cerasifera* Ehrh.) after 1 growing season (Symeonidou and Buckley 1999). WP has also shown positive correlation with RGP readings at outplanting for various hardwoods such as sugar maple (*Acer saccharum* Marsh.), silver maple (*Acer saccharinum* L.), paper birch (*Betula papyrifera* Marsh.), white ash (*Fraxinus americana* L.), black walnut, and northern red oak (Webb and von Althen 1980). In Symeonidou and Buckley's cherry study (1999), stem WP was compared with other physiological testing methods: REL, tetrazolium absorbance, and root moisture content (RMC). All methods were effective predictors of eventual plant performance. The main difference among the methods was cost effectiveness, with REL and RMC being the least costly. Tetrazolium testing and WP required more sophisticated equipment. In another comparative study, Radoglou and Raftoyannis (2001) evaluated REL, WP, and RMC of fine roots. For sycamore, flowering ash (*Fraxinus ornus* L.), and Spanish chestnut (*Castanea sativa* Mill.), REL values were significantly related to field performance of seedlings exposed to both freezing temperatures and desiccating conditions. WP and RMC were significantly predictive only in the desiccation treatment. Nutrient and foliar analysis, SIVE, and CF have been little used in the context of evaluating field performance potential of hardwoods, particularly because of problems associated with the deciduous nature of most hardwood species.

Future Directions

Future hardwood seedling quality research will face many challenges, but there are steps that can be taken to ensure successful and productive information exchange between practitioners and researchers. It is important to start with the most commonly produced species and consider the ability to transfer information to other species and families. However, it is likely that variable solutions exist for different species. Hardwood species also favor a number of different ecotypes. It is crucial to document site characteristics and replicate across other sites as needed. Lack of leaves is another consideration. It will be necessary to adjust timing and methodology of sampling procedures to account for this absence. An integrated approach to quality assessment will be needed to account for the many cultural and environmental variables responsible for changes in hardwood morphology and physiology.

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References

Bayley AD, Kietzka JW. 1996. Stock quality and field performance of *Pinus patula* seedlings produced under two nursery growing regimes during seven different nursery production periods. New Forests 13:337-352.

Belanger RP, McAlpine RB. 1975. Survival and early growth of planted sweetgum related to root-collar diameter. Tree Planters' Notes 26:1-21.

Curtis RO. 1955. Use of graded nursery stock for red pine plantations. Journal of Forestry 53:171-173.

Dey DC, Parker WC. 1997. Morphological indicators of stock quality and field performance of red oak (*Quercus rubra* L.) seedlings underplanted in a central Ontario shelterwood. New Forests 14:145-156.

Dickson A, Leaf AL, Hosner JF. 1960. Quality appraisal of white spruce and white pine seedling stock in nurseries. Forestry Chronicle 36:10-13.

Dunsworth GB. 1996. Plant quality assessment: an industrial perspective. New Forests 13: 431-440.

Duryea ML. 1985. Evaluating seedling quality: importance to reforestation. In: Duryea ML, editor. Evaluating seedling quality: principles, procedures, and predictive abilities of major tests. Corvallis (OR): Forest Research Laboratory, Oregon State University. p 1-6.

Edwards C. 1998. Testing plant quality. Farnham (UK): Forestry Commission, Forest Research Station. Forestry Commission Information Note 11. 6 p.

Gardiner ES, Russell DR, Oliver M, Dorris LC. 2002. Bottomland hardwood afforestation: state of the art. In: Holland MM, Warren ML, Stanturf JA, editors. Proceedings of a conference on sustainability of wetlands and water resources: how well can riverine wetlands continue to support society into the 21st century? Asheville (NC): USDA Forest Service, Southern Research Station. General Technical Report SRS-50. p 75-86.

Hallgren SW, Tauer CG, Weeks DL. 1993. Cultural, environmental, and genetic factors interact to affect performance of planted shortleaf pine. Forest Science 39:478-498.

Hashizume H, Han H. 1993. A study on forestation using large-size *Quercus acutissima* seedlings. Hardwood Research 7:1-22.

Hawkins CDB, Binder WD. 1990. State of the art seedling stock quality tests based on seedling physiology. In: Rose R, Campbell SJ, Landis TD, editors. Target seedling symposium: proceedings, combined meeting of the Western Forest Nursery Associations; 1990 Aug 13-17; Roseburg, OR. Fort Collins (CO): USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. General Technical Report RM-200. p 19-21.

Hawkins CDB, DeYoe DR. 1992. SIVE, a new stock quality test: the first approximation. Victoria (BC): Forestry Canada, FRDA Research Program Research Branch. FRDA Report No. 175. 24 p.

Jozefek HJ. 1989. The effect of varying levels of potassium on the frost resistance of birch seedlings. Silva Fennica 23:21-31.

King SL, Keeland BD. 1999. Evaluation of reforestation in the Lower Mississippi River Alluvial Valley. Restoration Ecology 7:348-359.

Kooistra CM, Bakker JD. 2002. Planting frozen conifer seedlings: warming trends and effects on seedling performance. New Forests 23:225-237.

Kormanik PP, Sung SS, Kormanik TL, Zarnoch SJ. 1995. Oak regeneration—why big is better. In: Landis TD, Cregg B, technical coordinators. National proceedings, Forest and Conservation Nursery Associations. Fort Collins (CO): USDA Forest Service, Pacific Northwest Research Station. General Technical Report PNW-GTR-365. p 117-123.

Kozlowski TT, Torrie JH, Marshall PE. 1973. Predictability of shoot length from bud size in *Pinus resinosa* Ait. Canadian Journal of Forest Research 3:34-38.

Landis TD. 1985. Mineral nutrition as an index of seedling quality. In: Duryea ML, editor. Evaluating seedling quality: principles, procedures, and predictive abilities of major tests. Corvallis (OR): Forest Research Laboratory, Oregon State University. p 29-48.

Lassheikki M, Puttonen P, Rasanen PK. 1991. Planting performance potential of *Pinus sylvestris* seedlings as evaluated by root growth capacity and triphenyl tetrazolium chloride reduction methods. Scandinavian Journal of Forest Research 6:91-104.

Lindqvist H. 1998. Effect of lifting date and time of storage on survival and die-back in four deciduous species. Journal of Environmental Horticulture 16:195-201.

Matsuda K. 1989. Survival and growth of konara oak (*Quercus serrata* Thunb.) seedlings in an abandoned coppice forest. Ecological Restoration 4:309-321.

Mattsson A. 1996. Predicting field performance using seedling quality assessment. New Forests 13:223-248.

McCreary DD, Duryea ML. 1987. Predicting field performance of Douglas-fir seedlings: comparison of root growth potential, vigor and plant moisture stress. New Forests 1:153-169.

McKay HM. 1992. Electrolyte leakage from fine roots of conifer seedlings: a rapid index of plant vitality following cold storage. Canadian Journal of Forest Research 22:1371-1377.

Michler CH, Woeste KE. 1999. Strategic plans for the Hardwood Tree Improvement and Regeneration Center. In: Dumroese RK, Riley LE, Landis TD, technical coordinators. National proceedings: Forest and Conservation Nursery Associations—1999, 2000, and 2001. Ogden (UT): USDA Forest Service, Rocky Mountain Research Station. RMRS-P-24. p 93-96.

Mohammed GH, Binder WD, Gillies SL. 1995. Chlorophyll fluorescence: a review of its practical forestry applications and instrumentation. Scandinavian Journal of Forest Research 10:383-410.

Mohammed GH, Noland TL, Parker WC, Wagner RG. 1997. Preplanting physiological stress assessment to forecast field growth performance of jack pine and black spruce. Forest Ecology and Management 92:107-117.

Moulton RJ, Hernandez G. 2000. Tree planting in the United States—1998. Tree Planters' Notes 49:23-36.

Nambiar EKS. 1984. Significance of first-order lateral roots on the growth of young radiata pine under environmental stress. Australian Forest Research 14:187-199.

O'Reilly C, Harper C, Keane M. 2002. Influence of physiological condition at the time of lifting on the cold storage tolerance and field performance of ash and sycamore. Forestry 75:1-12.

Orlander G, Rosvall-Ahnebrink G. 1987. Evaluating seedling quality by determining their water status. A test on a series of cold-stored *Pinus sylvestris* and *Picea abies* seedlings. Scandinavian Journal of Forest Research 2:167-177.

Pardos M, Royo A, Gil L, Pardos JA. 2003. Effect of nursery location and outplanting date on field performance of *Pinus halepensis* and *Quercus ilex* seedlings. Forestry 76:67-81.

Ponder F Jr. 2000. Survival and growth of planted hardwoods in harvested openings with first-order lateral root differences, root-dipping, and tree shelters. Northern Journal of Applied Forestry 17:45-50.

Radoglou K, Raftoyannis Y. 2001. Effects of desiccation and freezing on vitality and field performance of broadleaved tree species. Annals of Forest Science 58:59-68.

Reese KH, Sadreika V. 1979. Description of bare root shipping stock and cull stock. Toronto (ON): Ministry of Natural Resources. 39 p.

Ritchie GA. 1984. Assessing seedling quality. In: Duryea ML, Landis TD, editors. Forest nursery manual: production of bareroot seedlings. Boston (MA): Martinus Nijhoff/Dr W Junk Publishers. p 243-260.

Ritchie GA, Tanaka Y, Meade R, Duke SD. 1993. Field survival and early height growth of Douglas-fir rooted cuttings: relationship to stem diameter and root system quality. Forest Ecology and Management 60:237-256.

Rose R, Atkinson M, Gleason J, Sabin T. 1991. Root volume as a grading criterion to improve field performance of Douglas-fir seedlings. New Forests 5:195-209.

Ross-Davis AL, Broussard SR, Jacobs DF, Davis AS. Afforestation behavior of private landowners: an examination of hardwood tree plantings in Indiana. Forthcoming.

Ruehle JL, Kormanik PP. 1986. Lateral root morphology: a potential indicator of seedling quality in northern red oak. Asheville (NC): USDA Forest Service, Southeastern Forest Experiment Station. Research Note SE-344. 6 p.

Simpson DG, Ritchie GA. 1996. Does RGP predict field performance? A debate. New Forests 13:249-273.

Slocum GK, Maki TE. 1956. Exposure of loblolly pine planting stock. Journal of Forestry 54:313-315.

Stone EC. 1955. Poor survival and the physiological condition of planting stock. Forest Science 1:90-94.

Stone EC, Jenkinson JL. 1971. Physiological grading of ponderosa pine nursery stock. Journal of Forestry 69:31-33.

Sutton RF. 1990. Root growth capacity in coniferous forest trees. HortScience 25:259-266.

Symeonidou MV, Buckley GP. 1999. The effect of pre-planting desiccation stress and root pruning on the physiological condition and subsequent field performance of one year old *Prunus avium* and *P. cerasifera* seedlings. Journal of Horticultural Science and Biotechnology 74:386-394.

Templeton CWG, Colombo SJ. 1995. A portable system to quantify seedling damage using stress-induced volatile emissions. Canadian Journal of Forest Research 25:682-686.

Thompson JR, Schultz RC. 1995. Root system morphology of *Quercus rubra* L. planting stock and 3-year field performance in Iowa. New Forests 9:225-236.

Tinus RW. 1978. Production of container-grown hardwoods. Tree Planters' Notes 29:3-9.

Tomlinson PT, Buchschacher GL, Teclaw RM, Colombo SJ, Noland TL. 1996. Sowing methods and mulch affect 1+0 northern oak seedling quality. New Forests 13:191-206.

Wakeley P. 1948. Physiological grades of southern pine nursery stock. Society of American Foresters Proceedings 43:311-322.

Webb DP, von Althen FW. 1980. Storage of hardwood planting stock: effects of various storage regimes and packaging methods on root growth and physiological quality. New Zealand Journal of Forest Science 10:83-96.

Williams RD. 1972. Root fibrosity proves insignificant in survival, growth of black walnut seedlings. Tree Planters' Notes 23:22-25.

Ziegler EA. 1914. Loss due to exposure in the transplanting of white pine seedlings. Forestry Quarterly 12:21-33.