

ASSESSMENT OF SEEDLING VIGOR ATTRIBUTES:
OUTLINE FOR INTEGRATION

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Abstract. -- The demand for physiological tests of vigor will increase as seedling production becomes increasingly oriented to biotechnology, while the variability for morphological traits will decrease. Any measure of seedling vigor can be considered as a model of the seedling's future development. The time and structure hierarchy of physiological processes forms a basis for examining the underlying assumptions and implications of the measurements for a vigor model. An outline is proposed for a model incorporating morphological and physiological attributes of quality for the root system, the most readily manipulated part of nursery grown bareroot stock.

Additional keywords: acclimation, seedling morphology and physiology, structure and function.

INTRODUCTION

Seedling Stock Grading

The assessment of seedling quality from seed to a planted seedling is an essential part of stock raising and regeneration management. Seedling quality has proved difficult to describe in terms of measurable characteristics of the stock. "Quality is fitness for purpose" summarises the theme, but is too conclusive a definition to be operational. A measure of seedling quality should reflect a multitude of morphological and physiological characteristics.

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Morphological Characteristics

Morphological variables are attributes which describe structure and form attributes of seedlings, measured on a nominal scale (bud burst - no bud burst), an ordinal scale (stage of bud development in four classes), an interval scale (bud development stages have a measured difference) and a ratio scale (bud length). The measurement scale delimits the possible methods of analysis. Morphological characteristics can be manipulated in the nursery by altering seeding density, root pruning, transplanting, irrigation and fertilization. Morphological traits give an indication of seedling performance after planting out. The results on the correlation of seedling size to postplanting success are somewhat inconsistent (see Hermann and Lavender 1976 for a review). However, the use of morphological traits is extensive (Schmidt-Vogt 1980) and its adoption has improved the rating of seedling quality. Its major benefit lies in its ease of application on a large scale. Whenever the stock is subjected to heating, drying of roots, loss of moisture, or when the stock is planted on difficult sites, the planting success is even more influenced by the physiological condition of the stock (e.g. Schmidt-Vogt 1981).

Physiological Characteristics

Since Wakeley (1948) proposed physiological grading of nursery stock, with the purpose of defining seedling quality on the basis of internal chemical or metabolic properties, numerous physiological methods for planting stock grading have been proposed, tested, and applied. Such measures are the widely applied plant water status (Cleary 1971), electrical impedance (Glerum 1970), dead plant tissues (Zaerr 1972), food reserves (Krueger and Trappe 1967), mineral nutrients (van den Driessche 1971), hormones (Zaerr and Lavender 1980), root-growth potential (Stone 1955), stress resistance (Hermann and Lavender 1979), chlorophyll content of needles (Linder 1974), and CO₂ exchange (Troeng 1982). Irrespective of the objective of the assessment, these methods have been classified according to the measurement technique applied; physical parameters, quantitative chemical parameters, or an electrical test.

Results on the grading of seedling stock indicate that the physiological condition has a strong influence on survival and growth potential. Moreover, components of physiological condition are numerous and the physiological condition cannot be visually determined. Whereas the morphological traits are more easily assessed, the crux of defining the quality attributes of seedlings concerns physiological characteristics.

In this paper I will discuss the biological hierarchy of seedling quality attributes and draw conclusions regarding quality testing. Finally, I shall present an outline incorporating morphological and physiological characteristics of quality.

ORGANISATIONAL HIERARCHY IN PLANTS

In the biological sciences one can distinguish various levels of organization within plants; atoms and molecules, tissues, organs, plants, and populations. Mesarovic' and Macko (1969) have described the main properties of layered or hierarchially organized systems. Some of the main features are: 1) Each level has its own language, concepts, and principles. For instance, the term crop productivity has little meaning on the cell or organelle level. 2) Interpretation of a phenomenon at one level with reference to a lower level provides us with explanations, while interpretation with reference to a higher level hints at the significance of the phenomenon studied. 3) The relationship between levels is not symmetrical; a higher level requires accounting at all the lower levels in order to explain operation effectively, but not vice versa.

An other important hierarchy involves the temporal scale of plant physiological processes. Different levels of structural hierarchy are associated with processes possessing different response times to environmental variables (cf. Thornley 1980). The rate of photosynthesis can alter rapidly but changes in the rate of water uptake are slower. Also a physiological attribute can have several rates of change. Changes in leaf conductance are instantaneous but the change in maximum leaf conductance is slow, taking place through the conditioning of stomata. Physiological attributes change rapidly and independently of one another with time, and thus the period over which the data remain valid is short. Significantly, these changes, if precisely determined, can be used to determine critical phases in the production and handling of seedlings.

SEEDLING QUALITY AS A MODEL

A model is a formal statement of hypotheses which summarizes the knowledge of how a system at a particular level of organisation responds to environmental stimuli (Hall 1982). A measure of seedling vigor provides a model of the seedling's future development. Correspondingly, the measure of quality should be evaluated as a model structure. The model should provide consistent predictions of survival and initial growth over the expected range of field and seedling conditions. As

regards the testing of seedlings, the model is more concerned with management than with the mechanisms of the response. Explanatory models describe the internal function or regulation of a plant. Explanatory models are mechanistic and are tested with respect to internal consistency and overall prediction. Indeed, a model which is mechanistic at one level of organisation (e.g. the tissue level) is not mechanistic at a lower level (the cell or organelle level) (Hall 1982). Models built for managerial purposes are likely to be more useful and reliable if they incorporate mechanisms of the response (Landsberg 1981).

Transpiration and water relations are plant processes with a response time of seconds, minutes or hours. Correspondingly, the model of stomatal responses and leaf water relations, designed to reveal process rates is a very short-period model (level 1, Landsberg 1981). Integration of model responses on level 1 in space and time results in short period models (level 2) whose response times are hours and days. The outputs are hourly rates (e.g. transpiration) and daily totals or averages (e.g. average plant water status). The still longer period models at level 3 are mostly based on empirical relationships where the response time is in days or weeks. Shoot and root growth are examples of processes studied at this level. The structure and time hierarchy of physiological processes forms a basis for examining the underlying assumptions and implications of the measurements for a vigor model.

MEASUREMENT OF QUALITY CHARACTERISTICS

Morphological characteristics of seedling quality are measured as states at the plant level, e.g. shoot height and diameter of root collar. In practice, root collar diameter can be measured with an accuracy of one millimetre and even then is highly subject to measurement errors. In stock grading, the class interval of the root diameter is usually less than 1 mm. The class intervals are based on a larger sampling during the development of the classification. Statistically the classes can differ significantly. However, a difference of one millimetre in root collar diameter can correspond to a difference of 20 cm in shoot length. Therefore, I question the relevance of using the root collar diameter in grading.

Ritchie (1984) used the terms "performance" and "material attributes" as concepts in assessing planting stock quality. The performance attributes (root growth potential, frost hardiness and stress resistance) integrate the combined function of many physiological and morphological subsystems within the seedling. Material attributes (water relations, nutrition and seedling morphology) can be investigated by analyzing some of these

subsystems, e.g. carbohydrate concentrations of seedling components and leaf water potential. Although Ritchie (1984) classifies bud dormancy as a material attribute, it is normally evaluated as a performance attribute. Conversely, there is at present no direct material measure available for bud dormancy. The concept of material and performance attributes combines both state and rapid process variables of seedlings in a confusing manner.

Characteristics of physiological seedling condition are measured on plant or organ level and they often represent a process changing through time, e.g. water potential, transpiration, root growth potential, or speed of bud break all of whose response times differ. In a seedling test, the response of a process is studied as the state of a biological system at a given time instant. Thereafter the outcomes, e.g. leaf water potential and survival, of the two instants are correlated. However, the response time is totally different for a dying seedling than for the transpiration rate of a plant.

At a lower level of plant organisational hierarchy, measurements of seedling quality variables are carried out with devices which give estimates of fluxes between plant and environment, e.g. a porometer gives values for stomata conductance. The value of conductance may, however, be a process variable with a rapid rate of change, or in the case of maximum leaf conductance a state variable. At model level 2, the pressure-chamber technique is used to determine average plant water potential. However, weighted averages of the components of water potential lack physiological meaning (Weatherley 1970). Huss and Koch (1982) found that plant moisture tests made with the Scholander bomb had no forecasting value. At model level 3, rate of bud break and shoot growth are typical slow response processes studied e.g. in the stress test described by Hermann and Lavender (1979). Process variables quantify the rate of change of the state variables. Their values are determined by the state variables and knowledge of the underlying ecological, physiological and physical processes. Therefore, in physiological grading attention should be paid to identifying, measuring and interpreting the behavior of variables defining also physiological processes, as opposed to variables defining only a state.

In monitoring physiological quality characteristics of seedlings, measurements of state and process variables of plants should be synchronized with the environmental factors affecting quality. Many states and processes which are significant at smaller scales or lower levels may be irrelevant at a population level. Moreover, transmutations may occur when a process, or a function describing it, alters as one moves from one level of organisation to the next (O'Neill 1979). Therefore, the integration of small scale processes should be done with care, as

the assumption that a population responds similarly to the mean individual may not be warranted (O'Neill 1979). Nevertheless, the logical association of states and processes in the space-time scale helps in the formation of hypotheses and designing tests for significant relationships.

MODEL ACCLIMATION OF SEEDLINGS

Integration of Structure and Function

It has been recognized that exposure of a plant to one particular stress (e.g. heat) provides resistance to a stress of another kind (e.g. drought, Levitt 1972). This hints at the possibility that a single indicator of the planting stock could be used to evaluate vigor and to predict postplanting success of seedlings. A number of researchers have used heat stress to reflect drought resistance (Sullivan and Ross 1979, Hermann and Lavender 1979). Van den Driessche (1976) regards electrical tests in a similar manner. The dose and duration of a stress depends on the particular stress factor which renders the comparison and integration of different type of stress difficult. Kauppi (1984) presented a method to analyze the relationships between the fast stress variables and the slow injury variables.

There seems to be no single physiological or morphological trait of the seedling which would facilitate control over seedling quality. Morphological changes are too slow, and measures of physiological processes have a large proportion of error variation (poor signal-noise ratio) for the purpose of measurement. Nonetheless, physiological and morphological traits of seedling quality are inseparable since no physiological process can occur in the absence of a morphological anatomical basis. Wakeley (1948) cited evidence that morphological grades and physiological qualities do not necessarily coincide, nor are they necessarily identical with the plant's capacity to survive and grow. Therefore, it is prudent to integrate structure (morphology) and function (physiology) of a seedling as an entirety with the proper time response. Morphological traits describe the overall suitability of a seedling for a planting site but physiological traits describe the acclimation of the plant to the site.

The initial performance of forest plantations is the outcome of an interaction between the planted stock and its environment. The ability of seedlings to acclimatise to a planting site is crucial. As acclimation to the planting site is the ultimate test of seedling quality, the concept of planting

stock quality is deduced here from the physiology and early acclimation processes of the root system of the bareroot stock. Seedling characteristics which are known to influence planting performance are easily described but seldom combined into a quantitative approach. However, the model approach by Timmis (1980) must be recognized.

Model of Root Action

The development of the model starts with the specification of environmental, external and internal plant variables that influence root acclimation and growth at the planting site (here called root action). Next, the influence of individual variables on root action is determined at appropriate levels of the other variables. Thirdly, equations are developed to describe the effects of individual variables and their interactions. In the fourth stage, the values of input parameters are examined, e.g. by regression analysis. Fifth, the predictive ability of the root action model is tested with independent data. Finally, as the predictions of the model are likely to be imperfect, sources of error are analyzed and corrected. The whole process then repeated.

The characteristics of root action to be included in the model are root morphology (root area or length, root growth), plant water relations or their components (root water potential, hydraulic conductivity of root, evaporative demand, leaf mass), and soil-water relations (soil water content and/or potential, hydraulic conductivity of water). The model of root acclimation integrates essential root morphological and physiological attributes of plant water relations under the imperatives of environmental variables. The driving variables for the model, albeit at any level, are environmental factors.

The approach described would result in a phenomenological model (Jarvis 1976) of seedling quality which states the environmental and biological variables of the acclimation. It avoids the limitations of an empirical model in dealing with different environments. Characteristics of seedling growth, as well as the driving variables of growth, are functions of time, a fact which should be recognized in analyses. This may lead to a dynamic model (see Hari et al. 1983) of root action. In any case, the model should take into account the tempo of the environmental variables around a planted seedling.

Multiple correlation models based on the same variables of root morphology and physiology as in the dynamic approach, are static but relatively easily computed. This analysis could give weight ratios of importance for different morphological and

physiological variables included in the model. As a result, operational quality indices could be derived for specific conditions. The correlation model serves also as a step towards a dynamic root action model. The root action model has been outlined for bareroot seedlings, but a model can be developed for container seedlings by incorporating or modelling the acclimation of the shoot.

DISCUSSION

The root system is perhaps the most essentially manipulated component of the acclimated stock. Root growth characteristics (root growth potential, RGP or root regeneration potential, RRP) are significant as quality indicators (Burdett 1979, Ritchie and Dunlap 1980, Coutts 1981, Kauppi 1984). Many of the commonly employed root growth test methods are laborious except that proposed by Burdett (1979). Unfortunately, all test procedures involve inherent variability which precludes significant statistical and practical correlations of RGP or RRP to field performance (e.g. Sutton 1980). In addition, attempts at correlation imply a far greater control over the raising of seedlings at the nursery than it is currently imposed. Sandvik (1977) stated that the growing conditions in the nursery should be strictly controlled with respect to light, temperature, and physical properties of the growing medium if a defined physiological condition of the seedlings is to be achieved. A framework for this purpose is proposed by Räsänen (1980). It could have its data base in the computerized record maintenance of the nursery. The need for morphological grading will be much less in precision grown planting stock than in conventional non-uniform stock, but physiological grading will then be all the more important (Sutton 1979).

An ideal vigor index would be physiologically invariable with no dependence upon the environment. The rate of acclimation could be divided into two components, the driving variables and the internal plant properties. The internal properties could be separated from the effects of environmental variables enabling one to derive a "pure" quality index. This index would be independent of the environment.

Preconditioning techniques at the nursery can produce morphological, anatomical and physiological characteristics of seedlings that can promote the establishment of plantations. However, it still remains to be examined which are the conditioning processes best designed to prepare seedling stock for a particular environment.

There are considerable differences in the ease and relia-

bility of tests for measuring physiological characteristics of seedling vigor. Current physiological vigor tests require a considerable sample size for a chosen confidence level, which precludes rational and rapid analysis. The current use of a vigor test, whether morphological or physiological, implies that differences between seedling lots exist. If we cannot assume differences between lots, we would have to resort to testing seedlings on an individual basis. For example, the pressure-chamber technique would result in the destruction of large numbers of seedlings. A study of the variability of an attribute between seedlings and between seedling lots would make up a part of the analysis of variability for each phase of forest regeneration from seed to a sapling stand.

Further development of seedling vigor indecies may require us to conceptualize the quality term. "Quality is fitness for purpose" is a conclusive, posterior statement which needs to be developed into an operational, predictive statement. Models are accepted for controlling operational costs at the nursery. For shortening the trial and error sequence in the developement of quality standards, forest seedling producers should perhaps evaluate recent developments in the ecophysiological modelling of plants, too.

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