Testing Tree Seeds for Vigor: A Review

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ABSTRACT

This review examines the use of vigor tests for tree seeds. It suggests that precise evaluations of these tests and their application with seeds of woody plants is not yet possible. This is due to the wide genetic variation, primarily manifested in variable maturity and dormancy, that exists in most tree seed lots. Sensitive measurements of germination rate during standard germination tests have proved to be just as good, if not better, than any vigor test in judging the quality of seed lots. Accelerated aging, leachate conductivity, and germination rate all show promise, but extensive tests of field emergence are needed to validate the laboratory test procedures and interpretation.

INTRODUCTION

The evolution of vigor testing in agricultural seeds has been a slow, arduous, and still unfinished process (McDonald, 1993). Reaching agreement on a definition for "seed vigor" and which tests are suitable for each species, has been difficult. Nevertheless, the efforts of the AOSA Vigor Test Committee and many individuals in the organization bore fruit in the form of a "Seed Vigor Testing Handbook" (AOSA, 1983). This publication was preceded, by two years, by a similar handbook by the International Seed Testing Association (Perry, 1981) that was recently revised (Hampton and TeKrony, 1995). Both handbooks produced a consensus of definitions of seed vigor and both provided recommended and suggested vigor tests that are suitable for many of the major agricultural species of North America and the world. As several individuals were involved in the crafting of both handbooks, there are many similarities in the methods and recommendations. The process still continues, however, as new methods are devised and old ones are improved.

Neither of the vigor testing handbooks include recommendations for seeds of trees or of any other woody species. Based on current value of tree seeds alone, this is not surprising, but users of tree seeds (foresters, nursery managers, horticulturists, etc.) perceive a need for vigor testing of tree seeds and have encouraged tree seed researchers to pursue that goal. This review presents the published research on vigor testing of tree seeds, some unpublished data, and suggests which vigor tests show promise for operational use with tree seeds.

PAST WORK

A wide array of testing methods have been used to characterize seed vigor. Those tests that have been evaluated for tree seeds can be grouped into four types: seedling growth tests, stress tests, biochemical tests, and germination rate measurements.

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Seedling growth tests.

This vigor test involves germination under standard testing conditions and includes measurements of seedling size and/or weight, or classification of seedlings into vigor classes (weak vs. strong). Very little research with seedling growth tests has been reported for tree seeds. In a comparison of a several vigor tests with germination results in cherrybark oak (*Quercus* pagoda Raf.), mean seedling weights after 3 weeks in controlled environments (with and without light) were not significantly correlated with other seed performance parameters (Bonner, 1974). Vigor differences among samples were created with accelerated aging treatments, and no comparisons were made with field (nursery) performance. Germinator and greenhouse seedling growth tests with loblolly (*Pinus taeda* L.) and slash pines (*P. elliottii* Engelm.) yielded better correlations between mean seedling weight and other performance parameters, but standardization problems with the environmental conditions did not encourage further testing (Bonner, 1986).

Wang (1973) separated red pine (*P.* resinosa Ait.) seedlings into six vigor classes based on seedling development at the end of a laboratory germination test. A combination of Classes l-3 was significantly correlated ($r = 0.960$) with nursery seedbed emergence. Seedling Class 1 was defined as germinated with a healthy root, fully developed hypocotyl, and the seed coat completely shed. Class 2 was the same as class 1 except that the seed coat was nearly shed, while for Class 3 the seed coat was only partly shed. Wang (1976) used the same criteria on white spruce (*Picea glauca* (Moench.) Voss) with similar results; Classes l-3 were significantly correlated ($r = 0.896$) with soil emergence in a greenhouse test.

Stress tests.

Vigor evaluation by stress tests requires seed samples to be germinated either under stress conditions or under the standard germination test following a separate stress treatment. The cold test, the oldest vigor test in the United States (AOSA, 1983), and the cool germination test for cotton (Hampton and TeKrony, 1995) are examples of stress vigor tests with no reported uses on tree seeds. Such a void is hard to explain, since low soil temperatures plague forest nurserymen and at least one researcher has called for pine germination tests to be run at sub-optimum temperatures. (McLemore, 1969).

The one stress test that has received extensive testing among tree seeds is the accelerated aging (AA) test. Initially developed to evaluate storage potential of seed lots (Delouche and Baskin, 1973), it has evolved into an indicator of seed vigor in many agricultural crops. Seeds are exposed to high temperature and high relative humidity, factors that can cause rapid seed deterioration, and seed vigor is measured by subsequent germination testing. The differences in germination before and after aging provide a relative measure of seed vigor, but simple percentage differences lack the precision required for a real quantitative test. For this reason Wang et al. (1992) proposed the use an "Index of Aging" (AI) with lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.). AI is defined as initial germination % minus germination % after aging, divided by the initial germination. The need for precise control of the test environment and procedures (Hampton and TeKrony, 1995) makes the AA test more difficult than it may seem, but the basic concept of the test has been attractive to tree seed workers.

Most AA studies with tree seeds have focused on optimum times and temperatures for aging, which have been reported for a number of species (Table 1). Other tree species that have been tested, but had inconclusive results regarding AA conditions are: Sitka spruce *(Picea sitchensis* (Bongard.) Carriere) (Chaisurisri *et al*, 1993); white oak (Q. *alba* L.), cherrybark oak, sweetgum *(Liquidambar styraciflua* L.), sycamore *(Platanus occidentalis* L.), and green ash *(Fraxinus pennsylvanica* Marsh.) (Bonner, 1997). In a few studies, biochemical changes occured in the seeds during the aging treatments. Pitel (1982) aged seeds of jack pine (*P. banksiana* Lamb.) and northern red oak (Q. *rubra* L.) and followed changes in isoenzymes, amino acids, and proteins during aging. Blanche *et al* (1990) carried out similar tests with acorns of water oak (Q. *nigra* L.) and recorded changes in starch, reducing and nonreducing sugars, and amino nitrogen. Marquez-Millano *et al* (1991) followed changes in saturated and unsaturated fatty acids during aging of slash pine. The results of these biochemical studies clearly confirmed that rapid utilization of seed energy reserves during AA accompanied a decline in germination and seed vigor. This supports the concept that agricultural and tree seeds react in a similiar manner when subjected to AA conditions, which has eased concerns that

TABLE 1. Optimum accelerated aging treatment durations and outer chamber temperatures as reported in studies with tree seeds

Species	Temperature (°C)	Duration (hr)	Reference
Slash pine (*Pinus elliottii* Engelm.)	41	144	Blanche *et al*, 1988a
Longleaf pine (*P. palustris* Mill.)	41	96	Blanche et *al*, 1988a
Loblolly pine (*P. taeda* L.)	41	96	Elam and Blanche, 1990
Jack pine (*P. banksiana* Lamb.)	40	288	Downie and Wang, 1992
Lodgepole pine (*P. contorta* var. *latifolia* Engelm.)	40	288	Downie and Wang, 1992
White spruce *(Picea glauca* (Moench) Voss)	40	120	Downie and Wang, 1992
Pecan (*Carya illinoensis* (Wangenh. K.Koch))	41	144	Elam and Blanche, 1990
Water oak *(Quercus nigra* L.)	**41**	108	Blanche et *al*, 1990
Sissoo (*Dalbergia sissoo* Roxb.)	43	72	Thapliyal and Connor, 1997

seeds of woody plants might react strangely in tests designed for agricultural seeds.

Seed dormancy is one difference between some tree seeds and agricultural seeds that influence the interpretation of AA results. In many tests, short AA durations have increased the germination of tree seeds that normally exhibit dormancy (Blanche et al., 1988b, 1990; Bonner, 1984; Chaisurisri *et al.*, 1993). Possible explanations for this effect are that the aging treatments simply increase seed hydration to an optimum level (Bourland and Ibrahim, 1982) or that they provide a chilling-like effect of breakdown of polymeric storage compounds (Blanche *et al*, 1988b). Similar reactions have been reported for agricultural seeds without dormancy (Bourland and Ibrahim, 1982) and for tree seeds where aging treatments were initiated at high seed moisture levels (20%) (Bonner, 1984). Another possible explanation for increased germination in some tree species, is simply the result of immature seeds that are "pushed" to maturity by the aging treatment. This concept becomes more plausible if one considers dormancy to be just another manifestation of physiological immaturity.

Tree seed dormancy creates still another problem in vigor testing procedures. If seeds require chilling for standard germination tests (and field planting), should the chilling be done before or after the aging treatments? Research with a number of species clearly show that there is a difference in seed performance between chilling and no chilling following aging (Blanche et *al*, 1988b; Bonner, 1997; Wang, 1997). The more vigorous seed lots are usually stimulated by chilling after aging, while the opposite is usually true for the less vigorous lots. Vigorous seeds of non-dormant species do not show as much stimulation after post-aging chilling (Wang, 1997).

After considerable research on AA methodology for tree seeds, there is no apparent operational use for the test to determine seed vigor for nursery plantings. None of the above AA studies used seedbed emergence and growth to validate the AA measurements.

Another stress vigor test that has been studied sparingly is the methanol test (Musgrave *et al*, 1980). In this test seeds are hydrated, immersed in methanol/ water mixtures for 2 hours, and germinated as in the standard germination test. This test has been evaluated with seeds of rubber tree species in Indonesia (Sadjad, 1984) and more recently with four tree species in Mississippi (see the next section). The principle is the same as in accelerated aging; more vigorous seeds survive the stress treatment better than the less vigorous ones.

Biochemical tests.

The most widely known biochemical test is tetrazolium (TZ) staining. It is used to evaluate seed vigor in numerous agricultural seeds (AOSA, 1983; Hampton and TeKrony, 1995), and is frequently used as a rapid test to estimate of viability in dormant tree seeds (Enescu, 1991; Moore, 1985). On a limited scale TZ staining has been proposed as a vigor test on some tree species (Moore, 1964). Comparisons of TZ vigor estimates with other estimates of seed vigor have been made for loblolly, slash, longleaf (*P. palustris*

Mill.), shortleaf (*P. echinata* Mill.), Virginia (*P. virginiana* Mill.), and eastern white pine (*P. strobus* L.). In Mississippi these TZ results were not as highly correlated with seedbed emergence as were the estimates made by leachate conductivity and germination rate (Bonner, 1986, 1987).

Measurement of various solutes that leach from deteriorating seeds has attracted considerable attention in tree seed research, primarily because it provides a quantitative estimate of seed quality. Some studies have measured the amount of leached carbohydrates (Bonner, 1974) and amino nitrogen (Pitel, 1982), but most attention has been focused on leachate conductivity because of its simplicity, speed, low cost, and non-destructive nature. Attempts to relate seed vigor to single seed leachate conductivity of individual pine seeds were unsuccessful (Bonner, 1986; Bonner and Vozzo, 1983; Vozzo and Bonner, 1986). Thus, the single seed method was soon replaced with a bulk conductivity technique (Bonner, 1988) that was patterned after methods used on agricultural seeds (AOSA, 1983; Hampton and TeKrony, 1995). The bulk sample method did not provide a reliable prediction of performance of individual seed lots, but did provide a mechanism for sorting seed lots into four vigor classes (Table 2). Satisfactory results have been obtained with this classification for loblolly, slash, longleaf, eastern white, shortleaf, Virginia, Scotch (*P. sylvestris* L.), jack, and sand (*P. clausa* (Chapm. ex Engelm.) Vasey ex. Sarg.) pines (Bonner, 1991a, 1991b).

Perhaps the biggest problem with leachate conductivity as an indicator of tree seed vigor is the wide genetic variation that is present in seed lots that come from wild populations (natural stands). This was demonstrated in seed lots of red spruce (*Picea rubens* Sarg.) from the northeastern United States that were aged for various durations prior to measuring leachate conductivity (Bonner and Agmata-Paliwal, 1992). When a single seed lot was aged and tested, an exellent relationship was shown between conductivity and germination (R^2 = 0.970). When 14 and 38 seed lots were included in the prediction model, the R^2 value dropped to 0.530 and 0.286, respectively. The wider the genetic base, the weaker the relationship between seed germination and

TABLE 2. Seed quality classes of five pine species based on leachate conductivity measurements (after Bonner, 1991a)

Seed quality class	Approximate germination ranges†	Leachate conductivity				
		loblolly	slash	longleaf	shortleaf	eastern white
	(%)	µS g⁻¹				
High	85-100	<10	<5	<4.8	<9	<6
Medium	65-85	10-20	3-14	4.8-6.2	9-18	6-17
Low	40-65	20-34	14-25	6.2-10	18-35	17-40
Poor	<40	>34	>25	>10	>35	>40

†Includes dormant and empty seeds and abnormal germination for loblolly and eastern white pines.

leachate conductivity, which suggested that a reliable single model could not be established for a species that would predict all seed lots.

Other biochemical tests that have been evaluated for tree seeds include adenosine phosphate content, oxygen uptake of excised embryos and the glutamic acid decarboxylase activity (GADA) test of Grabe (1964). Bonner (1974, 1986, 1997) tested the latter two methods on cherrybark oak, sweetgum, sycamore, green ash, loblolly pine, and slash pine with little success and promise for future research. Ching and Ching (1972) measured adenosine phosphate content in germinating ponderosa pine (*P. ponderosa* Dougl. ex Laws.) and reported correlations with seed/seedling growth and morphogenesis. Ching (1973) later proposed adenosine triphosphate (ATP) content as a vigor test in crimson clover, ryegrass, and common rape, but did not extend this recommendation to ponderosa pine or to other tree seeds. Hopper et *a l* (1985) also reported that adenylate energy charge values could be related to seed vigor in northern red oak acorns, but no vigor test methodology was proposed.

Germination rate.

It has long been known that germination rate is positively correlated with rapid field emergence and seedling development in many species including tree seed. The most widely used method for tree seeds was developed by Czabator (1962). He proposed combining germination rate and completeness of germination of southern pine seeds from a laboratory test into a single numerical index that he termed Germination Value (GV). This index is determined by calculating the Peak Value (PV) (i.e. the maximum value of cumulative percent germination divided by the days of the test) and Mean Daily Germination (MDG) (the final percent germination divided by the total number of test days): GV = (PV) (MDG). Numerous studies have evaluated both GV and PV as indicators of vigor in tree seeds; however PV has proved to be more closely correlated with nursery performance in southern pines (Bonner, 1986, 1987). It should be pointed out however, that laboratory germination percent was just as good or sometimes better than PV or GV in predicting nursery emergence and seedling development in many pine species (Barnett and McLemore, 1984). Some other interpretations of germination rate have been proposed by Diavanshir and Pourbeik (1976) and Thomson and El-Kassaby (1993). These latter procedures have not been widely tested, but there is no reason to believe that they would not be successful for other tree species.

Other relatively simple parameters that reflect germination rate and have been evaluated with tree seeds include: percent laboratory germination through the peak day (Barnett and McLemore, 1984), number of days required to reach specified proportions of germination (Bonner and Dell, 1976), and mean germination time (MGT) of those seeds that actually germinated (Bonner, 1986). The latter parameter (MGT) has been proposed as a sensitive indicator of deterioration in wheat seeds (Dell'Aquila, 1987), and has given promising results with some tree seeds (Bonner, 1997).

Other evaluations of germination rate have employed more complicated mathematical models of test data. Campbell and Sorenson (1979) proposed probit transformations to study germination frequencies in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). This transformation produced linear models that were used to measure the time required to reach 50 percent (or other proportions) germination. Tests with southern pines, however, indicated that these models would not be linear if dormant seeds were present in the sample (Bonner, 1984). The three-parameter Weibull function was proposed as a model of germination test data to provide several parameters for vigor comparisons based on the frequency of germination (Bonner and Dell, 1976). Early experiments with the Weibull function as a vigor indicator in white oak and sweetgum were promising (Bonner and Dell, 1976), and the technique proved very useful in comparing germination data from four natural stands of sweetgum in Mississippi (Rink *et al*, 1979). More exhaustive testing of the Weibull model with loblolly and slash pines where nursery emergence was included in the studies suggested that it was no more sensitive to seed vigor differences than frequent counts of a standard germination test (Bonner, 1986). However, the success of counts was highly dependent on the frequency. If only two germination counts are made (i.e. an early count and a final count), the data will not be sufficient to measure germination rate. A minimum number of counts required per germination test is probably 10 (Bonner, 1986). At least three counts per week are needed, and perhaps more on rapidly germinating species. The data can be made more sensitive by using computer analysis to randomly distribute germination events to days on which no counts were made. For example, if germination is counted on Monday and Wednesday, the computer can divide Wednesday's count evenly between Tuesday and Wednesday, randomly assigning any odd germinant to one of the days. Germination rate parameters calculated with such data more accurately reflect the daily course of germination during the test.

ADDITIONAL EVALUATIONS OF VIGOR TESTS

Two recent experiments of vigor testing on tree seeds are presented to further explain the value of such tests. The first study of storage potential evaluated multiple seed lots of four species using several vigor tests. The seed was then stored for five years, retested and the vigor test data were examined to predict storage potential. In the second study, many Douglas fir seed lots were evaluated for germination and vigor and planted in industrial forest nurseries to determine nursery emergence in a series of field test plots.

Storage potential

Ten seed lots each of sweetgum, sycamore, loblolly, and slash pine were selected to provide a range of initial vigor from fresh and stored seed at the Forestry Sciences Laboratory, Starkville, Mississippi. Initial germination was measured on all seed lots following AOSA procedures. Samples were subjected to the following AA treatments and germinated: sweetgum and sycamore, 4 days at 40°C; loblolly pine, 43°C, 3 days and slash pine, 43°C, 4 days. At the end of the aging treatments, samples were germinated and leachate conductivity was determined on weighed 50-seed bulk samples immersed in 25 ml of deionized water for 24 hours. Conductivities were expressed as μSiemans g^{-1} of seed weight. One hundred seeds of each pine species were immersed in 20% (slash) and 30% (loblolly) methanol for 2 hours, then germinated as described for the Methanol test (Musgrave *et al.*, 1980). All remaining seeds were stored in air-tight plastic bottles in a walk-in refrigerator at 3 to 5°C for 5 years. Annual seed samples were evaluated for germination, but only the final (5-year) germination was related to results of the various vigor tests at the start of the storage period. Failure of refrigerator equipment led to the loss of some sycamore and slash pine seed samples. Thus, only sweetgum and loblolly results will be presented. Germination after 5 years was significantly correlated with initial germination and with stress test results for: accelerated aging (sweetgum, loblolly) and methanol stress for loblolly pine (Table 3). The highest correlations for sweetgum were with initial germination and PV following accelerated aging. For loblolly pine the highest correlations were initial germination percentage and germination percentage following methanol stress. There were no significant correlations between seed germination after 5 years storage and initial MGT or conductivity.

While both stress tests did provide strong indications as to which seed lots had good storage potential, the original germination test data were just as good or better. Setting initial standards of 85 percent germination and a PV of 3.5 for sweetgum and 90 percent germination and a PV of 5.0 for loblolly (both realistic for these species), would have identified all of the “best” seed lots, except two for sweetgum. This example, of course, is based to some extent on “second-guessing” the test results, but it indicates that standard germination results of these 20 seed lots were just as likely to enable an experienced seed analyst to predict storage potential as the results from the stress tests.

TABLE 3. Relationship between germination after 5 years of storage and initial germination and stress test parameters of 10 seed lots of sweetgum and loblolly pine. AA = accelerated aging; MEOH = methanol stress test; PNG = % normal germination; PV = peak value.

Dependent variable	Independent variable	R^2	p
sweetgum			
5-yr PNG	original PNG	0.658	0.004
5-yr PNG	AA PV	.611	0.008
5-yr PNG	AA PNG	.574	0.011
loblolly pine			
5-yr PNG	MEOH PNG	0.864	<0.001
5-yr PNG	original PNG	.847	<0.001
5-yr PNG	MEOH PV	.673	0.004
5-yr PNG	AA PNG	.651	0.005

Nursery emergence.

Samples from 32 freshly collected seed lots of Douglas-fir were tested for laboratory germination before and after accelerated aging at 41°C for 48 hours. Leachate conductivity was also measured on seed samples before and after aging according to Bonner (1991a). These lots were planted the following spring in two nurseries in the Pacific Northwest. Plots were established in the nursery beds and periodic counts were taken for seedling emergence and survival at the end of the growing season, which were regressed to initial seed germination and vigor test parameters.

Accelerated aging lowered mean germination by 48 percent (range of 20 to 92%) and PV by 4.7 (range of 3.6 to 7.7) over 32 lots. This indicated a wide range of seed quality, yet emergence results from the nurseries showed no significant relationship (Table 4) between performance in the seedbeds and the initial measurements of vigor by accelerated aging and leachate conductivity. The probable explanation of these poor correlations was that all of the seed lots performed well in the nurseries. One must conclude that although laboratory vigor tests indicated a substantial range in potential seed quality among seed lots, their immediate sowing and good care in the nursery avoided any losses in emergence. If the nursery had planted some of these seed lots immediately and stored other lots, the vigor test results could have been used to indicate which lots to store for planting in subsequent years.

CONCLUSIONS

Previous research suggests that vigor testing in tree seeds will never achieve the precision and levels of application present in vigor testing of agricultural seeds. This discrepancy is primarily due to the broad genetic base of most tree seed lots. This genetic base accounts for wide variations in the level of maturity at time of collection and in the degree of dormancy that is present in many species of woody plants. Collections from natural stands are the most variable, but even half-sib collections from single open-pollinated mother trees do not eliminate this problem. Vigor tests can still have a place in tree

TABLE 4. Correlations between vigor test measurements and nursery performance for 20 seed lots of Douglas-fir in an industrial nursery. AA = accelerated aging; LC = leachate conductivity; PNG = % normal germination; PV = peak value; A = differences before and after AA; GV = germination value.

	Dependent variables				
Independent variable	LC after AA	PV after AA	GV after AA	A PNG	APV
			R^2 (p)		
Emergence by June 22	0.033 (.442)	0.252 (.024)	0.278 (.017)	0.261 (.021)	0.113 (.147)
Live trees at Aug. 28	.045 (.369)	.253 (.021)	.024 (.514)	.257 (.022)	.109 (.156)

seed management, however, if expectations are in line with the capabilities of the tests. Based on the review of previous research and the new data presented in this paper, the following conclusions are presented:

1. For most tree species, especially for seed lots with good to excellent quality, a germination test that also provides a measure of germination rate is just as good, and often better, than any vigor test in judging the quality of the seed lot. When comparisons among seed lots are desired, PV (Peak Value) seems to be best. If treatments within a single seed lot are to be compared, MGT (Mean Germination Time) seems to be best.
2. When seed lots are intended for planting or storage for use in subsequent years, vigor tests can guide the decision as to which lots should be sown in the current season and which lots can be stored for later use without substantial losses in quality. Accelerated aging is the best test for use in these situations, although germination rate has proven to be just as good for many species.
3. Leachate conductivity, in spite of its simplicity, speed, low cost, and non-destructive nature, has not proven to be sensitive enough for anything other than half-sib family lots (narrow genetic base). If a seed lot is placed in long-term storage, as in germplasm conservation programs, leachate conductivity can be used to establish a baseline value. Periodic measurements in later years could be used to signal the deterioration of the lot. When seed lots have a wider genetic base, leachate conductivity can be used only to place individual lots into three or four vigor classes.
4. Several vigor tests described in this paper (accelerated aging, leachate conductivity, and germination rate measurements) have had adequate laboratory research on testing procedures. Before these tests will enjoy widespread use, they must show a closer relationship to field emergence tests. Seedling growth tests may deserve another look for some species, but must be integrated into the laboratory germination test to control costs.

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LITERATURE CITED

AOSA. 1983. Seed vigor testing handbook. Contribution No. 32 to Handbook on seed testing. Association of Official Seed Analysts. 93 pp.

Barnett, J.P. and McLemore, B.F. 1984. Germination speed as a predictor of nursery seedling performance. Southern Journal of Applied Forestry 8: 157-162.

Blanche, C.A., Elam, W.W., Hodges, J.D. 1990. Accelerated aging of *Quercus nigra* seed: biochemical changes and applicability as a vigor test. Canadian Journal of Forestry Research 20: 1611-1615.

Blanche, C.A., Elam, W.W., Hodges, J.D., Bonner, ET., Marquez, A.C. 1988a. Accelerated aging: a potential vigor test for longleaf and slash pine seeds. In: Proceedings 5th Biennial Southern Silvicultural Research Conference; 1988 November 1-3; Memphis, TN. Gen. Tech. Rep. SO-74. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station: 107-l 14

Blanche, C.A., Elam, W.W., Hodges, J.D., Bonner, F.T., Marquez, A.C. 1988b. Accelerated aging of selected tree seeds. In: Werrall, J., Loo-Dinkins, J., Lester, D.P., comp., eds. Proceedings 10th North American Forest Biology Workshop, Physiology and Genetics of Reforestation; 1988 July 20-22; Vancouver, BC. Vancouver, BC: University of British Columbia: 327-334.

Bonner, F.T. 1974. Tests for vigor in cherrybark oak acorns. Proceedings of the Association of Official Seed Analysts 64: 109-l 14.

Bonner, ET. 1984. New forests from better seeds: the role of seed physiology. In: Duryea, M.L. and Brown, G.N., eds. Seedling physiology and reforestation success. Proc. Physiol. Work. Group Tech. Sess., Soc. Amer. For. Conv. 1983. Portland, OR 16-20 Oct. Dordrecht: Martinus Nijhoff/Dr. W. Junk Publ.: 37-59.

Bonner, ET. 1986. Measurement of seed vigor for loblolly and slash pines. Forest Science 32: 170-178.

Bonner, F.T. 1987. Evaluation of seed vigor in longleaf, shortleaf, Virginia, and eastern white pines. In: Phillips, D.R., ed. Proc. Fourth Biennial Southern Silvicultural Research Conference. 1986 Atlanta. 4-6 Nov. Asheville, NC: USDA Forest Service Southeast. For. Exp. Sta. Gen. Tech. Rpt. SE-42: 77–80.

Bonner, F.T. 1988. Using leachate conductivity of bulked samples to estimate seed quality. In: Proceedings of the 1988 Southern Forest Nursery Association; 1988 July 25-28; Charleston, SC. Columbia, SC: Southern Forest Nursery Association: 164-172.

Bonner, ET. 1991a. Estimating seed quality of southern pines by leachate conductivity. Research Paper SO-263. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 4 p.

Bonner, ET. 1991b. Leachate conductivity: a rapid nondestructive test for pine seed quality. Tree Planters' Notes 42: 41-44.

Bonner, F.T. 1997. Unpublished data. Starkville, MS.

Bonner, ET. and Agmata-Paliwal, A. 1992. Rapid tests of seed quality in *Picea* species by the leachate conductivity method. In: DeHayes, D.H., Hawley, G.J., eds. Proceedings of the First Northern Forest Genetics Association Conference. 1991 July 23-25; Burlington, VT. Burlington: Univ. of Vermont: 69-75.

Bonner, F.T. and Dell , T.R. 1976. The Weibull function: a new method of comparing seed vigor. Journal of Seed Technology 1: 96-103

Bonner, F.T. and Vozzo, J.A. 1983. Measuring southern pine seed quality with a conductivity meter-does it work? In: Brissette, J.P. and Lantz, C.W., compl. Proceedings of the 1982 Southern Nursery Conferences. USDA Forest Service Tech. Publ. R8-TP4. Atlanta: USDA For. Serv. Southern Region: 97-105.

Bourland, F.M. and Ibrahim, A.A. 1982. Effects of accelerated aging on six cotton cultivars. Crop Science 22: 637-640.

Campbell, R.K. and Sorenson, EC. 1979. A new basis for characterizing germination. Journal of Seed Technology 4: 24-34.

Chaisurisri, K., Edwards, D.G.W., El-Kassaby, Y.A. 1993. Accelerated aging of Sitka spruce seeds. Silvae Genetica 42: 3033308.

Ching, T.M. 1973. Adenosine triphosphate content and seed vigor. Plant Physiology 51: 400-402.

Ching, T.M. and Ching, K.K. 1972. Content of adenosine phosphate and adenylate energy charge in germinating ponderosa pine seeds. Plant Physiology 50: 536-540.

Czabator, F.J. 1962. Germination value: an index combining speed and completeness of pine seed germination. Forest Science 8: 386-396.

Dell'Aquila, A. 1987. Mean germination time as a monitor of the seed ageing. Plant Physiology and Biochemistry 25: 761–768.

Delouche, J.C. and Baskin, C.C. 1973. Accelerated aging technique for predicting the relative storability of seed lots. Seed Science and Technology 1:427–452.

Diavanshir, K. and Pourbeik, H. 1976. Germination value-a new formula. Silvae Genetica 25: 79-83.

Downie, B. and Wang, B.S.P. 1992. Upgrading germinability and vigour of jack pine, lodgepole pine, and white spruce by the IDS technique. Canadian Journal of Forestry Research 22: 1124-l 131.

Elam, W.W. and Blanche, C.A. 1990. Accelerated aging: a potential vigour test for multipurpose tree seeds. In: Turnbull, J.W., ed. Tropical tree seed research. Proc. Int. Workshop. 1989. Gympie, Australia 21-24 Aug. Canberra: Austral. Centre for Int. Agric. Res.: 63-67.

Enescu, V. 1991. The tetrazolium test of viability. In: Gordon, A.G., Gosling, P., and Wang, B.S.P., eds. Tree and shrub seed handbook. Zurich: International Seed Testing Association. 9: l-19.

Grabe, D.F. 1964. Glutamic acid decarboxylase activity as a measure of seedling vigor. Proceedings Association of Official Seed Analysts 54: 100-109.

Hampton, J.G. and TeKrony, D.M. (eds.). 1995. Handbook of vigour test methods. 3rd Ed. Zurich: International Seed Testing Association. 117 pp.

Hopper, G.M., Parrish, D.J., and Smith, D.W. 1985. Adenylate energy charge during stratification and germination of *Quercus rubra*. Canadian Journal of Forestry Research 15: 829-832.

Marquez-Millano, A., Elam, W.W., Blanche, C.A. 1991. Influence of accelerated aging on fatty acid composition of slash pine (*Pinus elliottii* Engelm. var. *e llottii)* seeds. Journal of Seed Technology 15: 29-4 1.

McDonald, M.B. 1993. The history of seed vigor testing. Journal of Seed Technology 17: 93-100.

McLemore, B.F. 1969. Long stratification hastens germination of loblolly pine seed at low temperatures. Journal of Forestry 67: 419-420.

Moore, R.P. 1964. Tetrazolium testing of tree seed for viability and soundness. Proceedings Association of Official Seed Analysts 54: 66-70.

Moore, R.P. 1985. Handbook of tetrazolium testing. Zurich: International Seed Testing Association. 99 p.

Musgrave, M.E., Priestly, D.A., and Leopold, A.C. 1980. Methanol stress as a test of seed vigor. Crop Science 20: 626-630.

Perry, D.A. (ed.). 1981. Handbook of vigour test methods. Zurich: International Seed Testing Association. 72 pp.

Pitel, J.A. 1982. Accelerated aging studies of seeds of jack pine (*Pinus banksiana* Lamb.) And red oak (*Quercus rubra* L.). In: Wang, B.S.P. and Pitel, J.A., eds. Proc. Int. Symp. On Forest Tree Seed Storage. 1980. Chalk River, Canada 23-27 Sept. Ottawa: Canadian Forestry Service: 40–54.

Rink, G., Dell, T.R., Switzer, G., and Bonner, ET. 1979. Use of the Weibull function to quantify sweetgum germination data. Silvae Genetica 28: 9-12.

Sadjad, S. 1984. Personal communication. Dept. Of Agronomy, Bogor Agricultural University, Bogor, Indonesia.

Thapliyal, R.C. and Connor, K.F. 1997. Effects of accelerated aging on viability, leachate exudation, and fatty acid content of *Dalbergia sissoo* Roxb. seeds. Seed Science and Technology 25: 311-319.

Thomson, A.J., and El-Kassaby, Y.A. 1993. Interpretation of seed-germination parameters. New Forests 7: 123-132.

Vozzo, J.A. and Bonner, F.T. 1986. Using electrical conductivity of seed leachate as a measure of seed quality in southern pines. In: Proceedings of the International Symposium on Nursery Management Practices for the Southern Pines. 1985 Aug. 4-9; Montgomery, AL. Auburn, AL: Alabama Agriculture Experiment Station: 94–101.

Wang, B.S.P. 1973. Laboratory germination criteria for red pine (*Pinus resinosa* Ait.) seed. Proceedings of the Association of Official Seed Analysts 63: 90–106.

Wang, B.S.P. 1976. Dormancy and laboratory germination criteria of white spruce seed. In: Proceedings of 2nd International Symposium of IUFRO S2. 01. 06. on Physiology of seed germination. Fuji, Japan. 1976 18–30 Oct. Tokyo: Government Forest Experiment Station: 179-188.

Wang, B.S.P. 1997. Personal communication. Deep River, Ontario, Canada.

Wang, B.S.P., Downie, B., Wetzel, S., Palamarek, D., and Hamilton, R. 1992. Effects of cone scorching on germinability, and vigour of lodgepole pine (*Pinus contorta* var. *latifolia*) seeds in Alberta. Seed Science and Technology 20: 409–419.