

Climate change, forest mortality and need for a solid scientific foundation in forestry[†]

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[†] Presented at the 3rd International Electronic Conference on Forests – Exploring New Discoveries and New Directions in Forests (15–31 October 2022)

Abstract: Tree mortality is becoming more common in wild forests, plantations and orchards. Remedial or preventative counteracting measures are limited because, before onset of overt dying, reliable methods to distinguish intrinsically healthy from unhealthy trees are lacking. Survivotypes within dead populations can nevertheless be identified and conserved in support of achieving suitably adapted future forests.

Keywords: adaptation; afforestation; biodiversity; environment; fitness; forest dynamics; genetic diversity; landscape genomics; phenotype; reforestation; survivotype; tolerance; tree death

1. Introduction

Death of plantation seedlings and young previously healthy trees is recognized as an increasingly widespread response to environmental stresses arising from climate change. The causes of death are probably numerous but are often uncertain. Genotype - environment interactions are the general explanation for phenotypic variation, and phenotypes of varied survival fitness are here referred to as 'survivotypes.' Similar to morphological phenotypes, centuries of horticultural and physiological research have shown survivotypes to vary within species, subspecies, and geographic populations.

The challenge for the profession is to sustain healthy trees and forests, to have the best survivotypes for each location. The molecular genetics community has proposed a hypothetical way forward [1-4], asserting that "understanding the genetic basis of adaptation to the environment via landscape genomics studies is essential for management interventions of tree species related to conservation and reforestation under climate change [5]." However, it is uncertain if environments can be characterized reliably. Wild-type populations that were assumed to be well adapted are displaying widespread mortality. Moreover, some evidence indicates that landscape genomics lacks sufficient insight into tolerance [6].

If data on tolerance limits of survivors of wild-type mortality events were available for comparison with known (i.e., measured) limits of seedling stock intended for afforestation or reforestation, they would bolster genomics inferences and refine criteria used to choose stock capable of tolerating aseasonal changes and seasonal extremes.

2. Mortality, environmental change and survival fitness

Mortality in forest populations has been explained hypothetically in terms of trees becoming predisposed due to old age, or being externally incited into impairment of physiological health, or by biotic attack, hence resulting in weakening and a spiraling cascade of decline eventually leading to death [7]. There are innumerable factors to con-

Citation: Savidge, R.A. Climate change, forest mortality and need for a solid scientific foundation in forestry. *Environ. Sci. Proc.* **2022**, *4*, x. <https://doi.org/10.3390/xxxxx>

Academic Editor: Firstname Last-name

Published: date

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sider in these regards; Table 1 provides a general listing. Arborists know from long experience that once a tree is overtly in decline, mitigation and recovery is improbable.

Table 1. Some environmental factors associated with tree mortality

<u>Anthropogenic</u>	
Harvesting, land clearing, deliberate destruction	
Road salt, herbicides, over fertilization, toxic chemicals	
Soil compaction, root system severing	
Fire (deliberate, accidental)	
<u>Non-Anthropogenic</u>	
Soil movement: erosion, avalanches, landslides	
Soil flooding, freezing	
Lake outbursts, volcanic eruptions, glacier flow	
Tornadoes, hurricanes, ice storms,	
Radiation: heat, cold, sunscald, UV, fire (e.g., lightning)	
Water and nutrient deficiencies	
Mammals, birds, insects, nematodes, other small animals	
Fungi, bacteria, phytoplasma, viruses	

Tree death due to ‘old age’ alone is a physiologically nebulous concept. Viruses, mycoplasma, bacteria, fungal spores and other microorganisms settle upon scars following abscission and other types of wounding, and others enter with invasive animals. Some are believed to confer benefit while others produce toxins, digest cell walls, alter gene expression or otherwise compromise tree health [7-9]. Once internalized, microbial spread is checked or compartmentalized by endogenous antagonists, but a chronic struggle to remain healthy must prevail throughout the life of every tree. Resistance eventually declines, decay ramifies, and trees give the impression of dying of old age.

Although observations of widespread mortality in populations of young, seemingly healthy trees following drought, soil freezing, insect epidemics, etc., are becoming more common, some individuals inexplicably survive (Figure 1). At the other extreme, forest communities are healthy but isolated snags are nevertheless encountered. There are three plausible explanations: 1) trees of equivalent intrinsic fitness experience microsite variation in physical, chemical or biotic environmental factors; 2) microsite environment is uniformly constant, but intrinsic fitness varies; or 3) both intrinsic fitness and microsite vary. Environment comprises countless considerations, and fitness resides in both primary and secondary metabolism. So, excepting clonal populations of identical age, interactions between all possible combinations of fitness and microsite must be addressed to explain survival. This may appear to be a classic problem in genetics [10,11], but it involves an intractably huge number of poorly defined variables, beyond investigative capability for objectively unbiased discovery. More pragmatically, the genes, biochemistry and physiology of survivors could be compared alongside those of dying trees.



Figure 1. An example of widespread mortality in a young natural spruce forest. Note the survivors.

Knowledge and technology needed post-mortem to deduce cause of death are lacking, and reliable physiological methods for estimating and ranking the relative health status of living trees remain limited [12-14]. The overriding problem is that tree physiology knowledge remains far from complete, no matter which of the more than 70,000 tree species is considered. On the other hand, the facts that trees die within otherwise healthy communities and that rare individuals survive within populations undergoing general mortality can be viewed as opportunity to discover the fundamental basis for tree health, and thus for progress toward ensuring forest sustainability.

3. Survivotype tolerances and variation in intrinsic survival fitness

The extrinsic environment impinging upon trees and influencing intrinsic biochemistry and gene expression comprises a multitude of physical, chemical and biotic phenomena, each of which by its variable and often unpredictable nature tests fitness. There can be no doubt that those phenomena have existed throughout the 394 million year history of trees [15]. In other words, trees have evolved to tolerate changing environment, but precisely how they do so remains far from well understood. Statistically supported trends derived from observations on permanent sample plots and plantations, and unstated assumptions about future environment, have detracted from performance of fundamental research to reveal the intrinsic basis for and limits of tolerance. The unexpected loss of large numbers of trees is an awakening, challenging us to advance understanding of all that affects tree health and determines the strengths and weaknesses of trees.

Forest scientists have investigated populations and communities, trying to understand how they function and change. However, conservation of survivotypes having exceptional fitness remains to become a priority. Tree scientists have investigated sub-cellular phenomena in efforts to understand how extrinsic factors influence growth, development, reproduction and phenological variation, but only now is it being recognized that having increased knowledge about variation in the ranges and limits of tolerance is crucial for sustainability of the terrestrial biosphere.

Based on what is presently known, a reasonable hypothesis is that at least some survivors in wild-type populations are in possession of exceptional tolerance limits. If research can confirm that, elucidation of the underlying physiological, biochemical and genomic information within those survivotypes would contribute to forest sustainability and also provide needed precision for landscape genomics to make reliable recommendations. Research is needed such that the knowledge becomes pragmatically useful.

Tree improvement programs began early in the 20th century, and at the outset there was a focus on discovery of variation in environmental tolerance [16,17]. However, that faded, not only because of an emphasis on commercial gain but also because it seemed obvious (on the assumption that the environment would remain constant) that trees demonstrably superior in commercial attributes were at least equal to wild types in survival fitness. Consequently, persuasive evidence for selected stock having survival fitness equivalent to that of wild types remains to be provided. What if fast-growing trees are actually less fit? For example, photosynthate is essential for growth, but it also is used in biosynthesis of storage reserves and production of secondary metabolites of defense. If storage reserves and secondary metabolites are insufficient, "improved" though relevant to commerce may be a misnomer in relation to the greater concern of sustainability [18].

The stage has long been set to undertake seedling testing for discovery of tolerance ranges and limits using various types of controlled environment chambers [19,20]. Advances in high resolution satellite imagery have made it possible to identify mortality events in progress, also the precise locations of survivors [21]. What is needed now is an entirely new tree science program in support of teams of field personnel, remote sensing technicians, physiologists, biochemists, molecular biologists, population geneticists, laboratory, greenhouse and nursery technicians, and more. Such a program will require no small undertaking, nor should it if there is to be any genuine confidence in the ability of humanity to sustain the terrestrial biosphere in a forested state.

4. Summary

A paradigm shift in tree-improvement programs is proposed, such that long overdue data become used to develop criteria enabling identification of suitably adapted stock for reforestation and afforestation of targeted geographic regions globally. Those data could be gained through investigations by tree scientists of mortality survivotypes and by determination of tolerance limits of putatively improved seedlings,

Acknowledgments: University of New Brunswick Libraries made literature available. This research received no external funding. Any errors or omissions are the author's.

Conflicts of Interest: The author declares no conflict of interest.

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