environmental sciences proceedings

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Proceeding Paper

Climate Change, Forest Mortality, and the 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; Available online: https://iecf2022.sciforum.net/.

Abstract: Tree mortality is becoming more common in wild forests, plantations, and orchards. Remedial or preventative counteracting measures are limited because, before the onset of overt dying, reliable methods to distinguish intrinsically healthy trees 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

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Citation: Savidge, R.A. Climate Change, Forest Mortality, and the Need for a Solid Scientific Foundation in Forestry. *Environ. Sci. Proc.* **2022**, *22*, 44. https://doi.org/10.3390/IECF2022-13072

Academic Editor: Rodolfo Picchio

Published: 17 October 2022

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 referred to here 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 the 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 consider in these regards; Table 1 provides a general listing. Arborists know from long-held experience that once a tree is overtly in decline, mitigation and recovery is improbable.

Table 1. Some environmental factors associated with tree mortality.

Anthropogenic
Harvesting, land clearing, deliberate destruction
Road salt, herbicides, over fertilization, toxic chemicals
Soil compaction, root system severing
Fire (deliberate, accidental)
Non-Anthropogenic
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 benefits 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) the microsite environment is uniformly constant, but intrinsic fitness varies; or (3) both intrinsic fitness and microsite vary. The 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.

The knowledge and technology needed post-mortem to deduce the 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 fact that trees die within otherwise healthy communities and that rare individuals survive within populations undergoing general mortality can be viewed as an opportunity to discover the fundamental basis for tree health, and thus for progress toward ensuring forest sustainability.

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

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 environments, but precisely how they do so remains far from being well understood. Statistically-supported trends derived from observations on permanent sample plots and plantations, and unstated assumptions about future environments, have detracted from the performance of fundamental research to reveal the intrinsic basis for and limits of tolerance. The unexpected loss of a large numbers of trees is an awakening, challenging us to advance our 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 with exceptional fitness is still 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 the 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 this, 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 the discovery of variation in environmental tolerance [16,17]. However, this focus 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 with a 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 the biosynthesis of storage reserves and the production of secondary metabolites of defense.

If storage reserves or secondary metabolites are insufficient, "improvements" 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 the 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, and 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 are 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.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

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

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

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