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The rise of the mediocre forest: why chronically stressed trees may better survive extreme episodic climate variability

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Abstract Anthropogenic climate change is a relatively new phenomenon, largely occurring over the past 150 years, and much of the discussion on climate change impacts to forests has focused on long-term shifts in temperature and precipitation. However, individual trees respond to the much shorter impacts of climate variability. Historically, fast growing, fully canopied, non-chronically stressed (NCS) trees (e.g., those with minimal insect or disease damage, growing on high nutrient, moist soils), have been considered the model of individual health, while slower growing, broken crown, chronically stressed (CS) trees growing on nutrient poor, or dry soils, were considered to be unhealthy and prone to stress related mortality. Over the coming years and decades, climate variability (e.g., extreme precipitation events, drought, heat waves) is expected to increase. We hypothesize that as the duration, severity and interaction of stress becomes more pronounced under increasing climate variability, seemingly less healthy, CS trees could begin to survive environmental stress better than their traditionally considered healthy, NCS tree counterparts. We further hypothesize that this shift in survivorship will be attributed to tree response to increasingly extreme climate variability at levels not previously observed in recorded history. While NCS trees can better survive historic episodic stress, we hypothesize that CS trees may be better suited to survive the combination of chronic low-level stress, and extreme episodic stress associated with anthropogenic climate change and increasing climate variability. Specifically, morphological differences such as increased root and reduced leaf mass, and physiological differences such as more oleoresin production, could make slower growing, CS forests more resilient to catastrophic episodic mortality compared to more NCS stands under certain circumstances. General circulation models suggest that climate variability will increase in the future. Therefore, the occurrence of slow growth, CS forest stands out surviving faster growing NCS less stressed stands may become more common place, and eventually lead to "The Age of the Mediocre Forest". This paper addresses the type of environmental conditions that could create such an inverse in forest health conditions, and the implications that this shift might have in forest genetics and management.

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Introduction

The dominance of a tree species based on pollen records indicates that each species' relative success varies in response to changing environmental conditions. For instance, during glacial periods across the region corresponding to modern day US and Canada boundaries, firs (*Abies* sp.) and spruce (*Picea* sp.) were prevalent, while oaks (*Quercus* sp.) and hickories (*Carya* sp.) were present in greater numbers during warm dry periods (Johnson 1999). These changes in species dominance historically occurred over many millennia, and generally involved long-term slow shifts in climate (IPCC 2007). However, the advent of the Industrial Revolution caused more rapid environmental changes, including changes in the atmospheric carbon dioxide (CO_2) concentrations. From approximately 1850 to present, fossil fuel burning has raised the average annual atmospheric CO_2 concentration from 270 parts per million (ppm) to current levels approaching 400 ppm (IPCC 2007), a 33 % increase. The increase in atmospheric CO_2 has been correlated with increases in air temperature and climate variability during this time period (IPCC 2007).

As the twentieth century closed, the impacts of climate change on forest productivity and mortality became more clearly defined. Thompson et al. (2009) identified major biomes that would have greater or lesser resilience and resistance to climate change. Clavel et al. (2011) further refined the relative forest winners and losers of climate change impacts at the functional group level. For example, drought and fire tolerant tree species appeared to be better able to adapt to the increasingly unstable environmental conditions, while more specialized species appeared to be on the decline (Clavel et al. 2011). Kominoski et al. (2013) continued to refine this area of study by examining the functional implications of global change on riparian plant communities.

If survivability is changing between species and functional groups, then we hypothesize that climate variability may also be changing intra-species survivability. Specifically, we wanted to consider if the trends in survivorship between non-chronically stressed (NCS) and chronically stressed (CS) trees and forest stands within the same species could be changing in association with changing climate variability. We define historically, fast growing, fully canopied trees with minimal insect or disease damage, growing on high nutrient, moist soils, as NCS. Conversely, slower growing, broken crown, trees growing on nutrient poor, and dry soils are defined as CS within this paper. Likewise, the interactions between climate variability and other environmental stresses such as insects, and pollutants on individual trees may change. If so, then the silvicultural practices and tree genetic manipulation objectives and goals may also need to change as a result. This paper hypothesizes a potential mechanism for how CS forested may have lower rates of mortality compared to NCS forests under increasingly frequent and severe episodic climate induced ecosystem stress. We will use a case study to suggest the mechanisms for this mortality class shift, and suggest how forest management and genetic research could be modified to adapt with changes in climate variability.

Traditional definition of a healthy tree

Traditionally, heavily stocked (i.e., high basal area) forests comprised of large, full crowned, fast growing trees showing minimal insect and disease damage have been considered the model of forest health. For decades, commercial forestry operations have focused on creating such forests through the use of genetically improved growing stock, fertilization, and silvicultural practices (Allen et al. 1990; Fox 2000; Jayawickrama 2001; Sutton 2002). However, under anthropogenically induced climate change, long held notions regarding the definition of a healthy forest may break down, and the definition of a healthy forest may need to be reassessed. We hypothesize that trees at the individual level and stands at the tree community level may be responding in previously unobserved ways in response to the previously unobserved changes in climate variability. As the response of trees change, we hypothesize that forest structure and function could also change. If these conditions are true, then the practice of ecosystem management may also need to change.

As a whole, natural and managed trees may be adapting to changes in climate, but in ways that were not previously envisioned. This paper hypothesizes how climate variability could change traditional notions of tree and therefore forest health. These questions may have added significance to species growth and response variability as forest geneticists seek to improve growth rates, resilience and resistance of commercially important tree species to stress. Therefore, we asked "could improvements in tree performance make forests more susceptible to an increasingly variable climate?"

For example, geneticists have a long history of improving loblolly pine (*Pinus taeda*) stocks across the southeastern US. Dorman and Zobel (1973) identified genetic species variation across the region. Seed collection, and propagation of these individual trees were designed to match those areas where specific varieties of loblolly pine have historically done well with regards to disease (Wakeley and Bercaw 1965), drought resistance (Dorman 1976), or cold tolerance (Wells 1969).

Agents of forest change

Weather is constantly changing, but climate (barring an environmental catastrophe such as an asteroid impact or massive volcanic activity) has historically been considered stable in the (geologic scale) short term of decades to centuries (Hegerl et al. 2007). In addition to the prevailing climate associated with a geographical location, patterns of unusually hot, cold, wet or dry weather may persist for months (e.g., El Niño/La Niña periods, Penland et al. 2010). The combination of seasonal and episodic weather variability constitutes the climatic regime of an area. Many studies have documented changes in historical weather patterns associated with climate change. Growing seasons are becoming longer, night time air temperatures are warmer, and precipitation events are becoming more extreme (IPCC 2007). Expectations of tree response to climatic conditions are based on historic observations of individual tree and forest tolerance to stress. If climatic conditions change to a degree that tree response to these stresses change in a previously unobserved manner, then the definition of a healthy tree or forest may also need to change.

Competition

At the species level, trees have evolved to best utilize, and therefore compete for the existing resources within their climatic range. Drought tolerant species such as hickory (*Carya* sp.) can successfully become established, grow and reproduce in dry, unfertile hill slopes where other water and nutrient demanding species such as sweetgum (*Liquidamber styraciflua*) would have a competitive disadvantage. Conversely, in moist and fertile bottomland soils, sweetgums relatively fast growth rate would rapidly overtop and suppress any hickory trees trying to become established in that same area. Thus, each species has an established niche within the landscape.

Within the same forest stand, rapidly growing trees have historically had a competitive advantage over their slower growing counterparts for many reasons. The ability for rapid growth provides increased opportunities for maximizing individual tree access to sun light at the top of the canopy (Kempes 2011). As dominant tree growth increases, leaf mass, stem, and crown diameter increases (Martin et al. 1998). By default, the increase in resource use by a dominant healthy tree reduces the resource base of the sub-dominant trees which further stresses non-dominant trees. Historically, the loss of resources to the sub-dominant trees could remove these individuals as a resource competitor through mortality, or at least minimize the sub-dominant tree impact on water, nutrient and sun light resource use until such a time when the canopy structure is altered through disturbance (e.g., wind, fire, lightening, or insect).

Thus far, this paper has discussed historic levels of environmental stress. However, climate change and variability may significantly extend the historic range of environmental stress. Droughts, heat waves, insect outbreaks, wild fires may become longer and/or more severe. Our observations of plant response to stress are based on historic precedent. If climate change moves beyond our previous observation point, then plant response to these stresses could also move beyond our previous observation point. We are not suggesting the plants and ecosystems will deviate from their prehistoric response to stress, but only that is no recorded history of ecosystem response to this extreme climatic variability. We hypothesize that under the combination of chronic and extreme episodic climate stress, CS ecosystems will have lower rates of mortality than NCS ecosystems, and we use the following case study to illustrate the reason for this theory.

A case study of natural stand response to episodic and chronic stress

The case study was derived from a forested area within the southern Appalachian Mountains. This is the first mountain range to come in contact with the northeastward air flow from the Gulf of Mexico. The moisture laden gulf air generates large amounts of precipitation across western North Carolina, while the mountainous terrain keeps air temperatures low relative to other parts of the southeastern US (McLaughlin et al. 1987). The high annual rate of precipitation and elevational range of the Appalachian Mountains keeps the region among the most biologically diverse in North America (SAMAB 1996). Part of that diversity includes the most southerly extent of red spruce (*Picea rubens* Sarg.) in the eastern US. (SAMAB 1996; Sullivan 1993).

Mount Mitchell, North Carolina including Mount Mitchell State Park is located within this area, and was founded in 1915 after the forest had been heavily logged. Given that logging has not been permitted within the park since establishment, most of the mature forest including the red spruce originated during the 1920s (Silver 2007). The forest has received minimal forest management since the time of establishment.

The National Climatic Data Center (NCDC 2014) reported that between 1950 and 1995, the area around Mount Mitchell received 650 mm (s.e. 165) of average growing season (i.e., May–August) precipitation, and growing season air temperature averaged 13.2 °C (s.e. 0.63 °C; Fig. 1). However, from 1996, 2000, the average growing season precipitation was reduced to 510 mm (s.e. 95 mm; Fig. 1), while average growing season air temperature

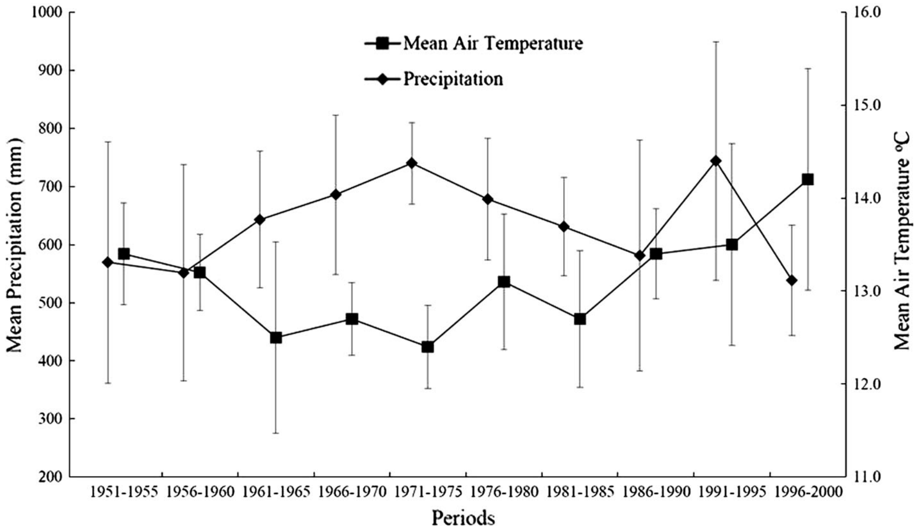


Fig. 1 Mean annual growing season air temperature and precipitation on Mount Mitchell for 10 periods, starting with 1951–1955 and ending with 1996–2000. Each period is an average of five years of record

increased to 15.2 °C (s.e. 1.2 °C; Fig. 1). The 1996–2000 period represented the most extreme fluctuation in climate to this area in over the past half-century (NCDC, 2014; Fig. 1).

Drought and elevated air temperatures were not the only stresses on the red spruce ecosystem at that time. The Southern Appalachian Mountains are under chronic stress from ozone, and acidic (i.e., nitrogen and sulfur) deposition (McLaughlin et al. 1987). Parts of the Southern Appalachian Mountains receive some of the highest rates of acidic deposition in the eastern United States, but these levels are considered to be below the critical acid load that would cause forest damage (McNulty et al. 2007). Also, southern pine beetles (*Dendroctonus frontalis* Zimmermann) are an endemic pest of the southern US that normally infest southern pine species, especially loblolly pine (*Pinus taeda*). However, the unusually warm air temperatures around Mount Mitchell between 1996 and 2000 allowed the predominately lower elevation southern pine beetle to move into the temporarily warmer upper elevation red spruce forest (McNulty and Boggs 2010).

It was under these environmental conditions, that during the 1996–2000 drought, some stands of red spruce around Mount Mitchell began to die following a southern pine beetle infestation, while other red spruce appeared to withstand the attack and survive within the same general area (McNulty unpublished). A field investigation indicated that there were significant individual and ecosystem level differences between the red spruce that were killed and survived the southern pine beetle outbreak (McNulty unpublished). The few surviving spruce in the area with predominantly dead trees had statistically higher ($P < 0.05$) foliar percent nitrogen (N) concentrations compared to those trees from areas with low rates of tree mortality. Also, the sites with highest tree mortality had lower forest floor carbon to nitrogen (C:N) ratios. Nitrogen is often the most growth limiting soil nutrient as atmospheric CO_2 concentrations rise (Norby et al. 2010). A low C:N ratio is an indicator of high soil nitrogen fertility, and high growth potential (Vitousek and Howarth 1991).

Basal core samples were taken from the stem (1.5 m above the forest floor) of both living and recently dead trees. The corers were sectioned into 5 year increments, and measured for basal area growth and wood tissue isotopic carbon concentrations. The area where the beetles killed the dominant red spruce had higher long-term (1950–2000) basal area growth rates ($P < 0.001$), and had lower wood tissue isotopic C^{12} and C^{13} than did the area with trees that survived the drought and beetle attack (McNulty, unpublished).

Atmospheric C^{12} and C^{13} isotopes are taken into plants through the stomata as CO_2. As soil conditions progress from moist to dry, the stomata begin the close and the relative incorporation of C^{12}:C^{13} assimilation changes within the tree growth rings. By counting growth rings, and measuring the tissues C^{12}:C^{13}, it is possible differentiate trees that are more or less water stressed (McNulty and Swank 1995). From an analysis of these measurements, we were able to determine that the trees that were the most vigorously growing for decades under a normal range of climatic conditions were the ones most likely killed during the drought and beetle outbreak.

Hypothesis for the higher survival rate of CS trees compared to NCS trees during extreme episodic stress

The biometric and meteorological data suggest that a series of episodic disturbances (i.e., 3 year drought, abnormally high air temperatures, and the presence of the beetles) and chronic stress (i.e., elevated nitrogen deposition) combined to make the NCS trees much more susceptible to perturbation than would have been expected based on long-term stand growth data and visual observations. We hypothesize that long-term nitrogen deposition and increased soil C:N likely reduced the root/shoot ratio (Aber et al. 1989) of the NCS trees. This condition would not have normally stressed the trees given that the area usually receives a high rate of rainfall. To the contrary, the sites with the highest rates of beetle caused mortality historically had the highest rates of forest growth, likely due to increased leaf biomass relative to the CS spruce trees (McNulty and Boggs 2010). As the drought developed, the increased relative demand for water due to increased leaf area coupled with the reduced relative root biomass to supply the water could have significantly stressed the NCS trees more than slower growing CS trees. Mattson and Haack (1987) observed that a lack of soil moisture can significantly reduce oleoresin production and flow, and increase insect colonization (Mason 1971). Conversely, the CS trees (having lower foliar % N, and high forest floor C:N ratios), did not experience the same level of insect caused tree mortality. This suggests that under these extreme environmental conditions of low precipitation and high drought, the trees that would historically be considered the most healthy and productive (i.e., NCS) were actually more at risk to mortality than the slower growing, CS stand (Fig. 2).

Although the exact mechanism for this inversed resiliency requires further study, we hypothesize that two preceding conditions may have contributed to this anomalous result. First, the trees growing on the poorer quality sites likely allocated proportionately more energy toward below ground roots in an attempt to fully utilize the limited existing water and nutrient resources as found in other studies (Kleczewski et al. 2010, 2012; Urban et al. 2013). However, a difference in the allocation of carbon between NCS and CS stands may not in itself fully explain difference in tree mortality rates between those with high and low chronic stress.

Given that resources (i.e., water, light, nutrients) are not evenly distributed within a stand, with dominant individuals general acquiring more of the resource compared to the suppressed individuals, we hypothesize that within the CS stand, the prolonged (3 year) episodic drought killed some of the most limited resource individual trees prior to the insect infestation (Fig. 2). Observations in the CS area revealed some recently dead (indicated by the

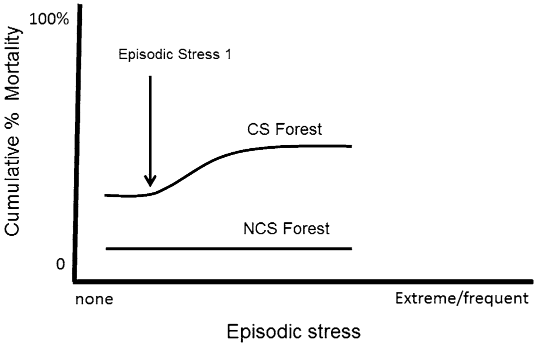


Fig. 2 Observed historic relationship between ecosystem stress and forest mortality under CS and NCS forest conditions

bark still firmly attached to bole, but loss of foliage) trees without evidence of insect boring (indicated by the lack of bore holes and wood particulates around the tree bole). The loss of the very weakest trees within the CS site may have liberated sufficient resources (mainly soil water) to allow the remaining trees on the CS area to survive the subsequent beetle attack and continued drought (Fig. 3). The reduction in competition through partial stand mortality was not observed in the NCS area prior to the insect attack because no dead trees were found that did not also have insect infestation markings.

Projected future trends in CS and NCS forest health

The conditions necessary for the CS tree survival to exceed that of NCS trees (as described in this study) would currently be considered a rarity (Fig. 3). We hypothesize that during relatively minor episodic stress events (e.g., moderate drought), NCS stands would not routinely die, but CS trees may experience some mortality as the trees are already CS (e.g., due to poor soil conditions, or chronically limited precipitation; Fig. 2). The limited mortality in the CS trees could temporarily relieve the stand level resource demands, and provide a buffer for additional stress. During a second (and possible more severe) episodic stress (e.g., severe drought combined with an insect outbreak), the combination of the more CS adapted morphology of the CS trees, coupled the reduced resource demand (as a function of the previous limited tree mortality) could allow the CS stands to better survive these extreme conditions compared to the NCS stands (Fig. 3).

Global warming is associated with many environmental changes including changes in precipitation timing, distribution and amount (Karl et al. 1995; Dore 2005; IPCC 2007). As climate change progresses, forests are expected to experience an increase in the severity and duration of droughts, and heat waves and other chronic ecosystem stress (Fig. 4, IPCC 2007). Therefore, NCS forests could more commonly become at increasing risk for extreme episodic or synergistic disturbance. If this is the case, then episodic stress may cause more mortality on NCS trees than on CS trees. We term this condition the *inverse risk point* in which a combination of chronic stress, tree morphological response to chronic stress; and the timing and severity of episodic stress interact in such a way that the NCS trees become more susceptible to mortality than do CS trees (Fig. 3) as was experienced in this case study.

Thus, the increase in climate change variability, coupled with associated stress from other ecosystem components (e.g., insects and disease outbreaks, invasive species, and wildfire) may support *The Age of the Mediocre Forest* as previously unobserved extreme

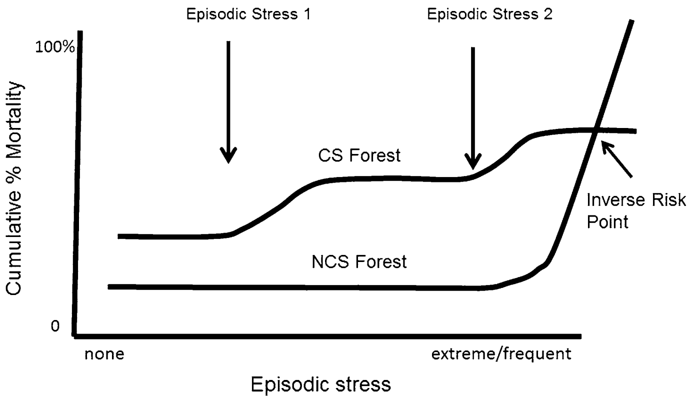
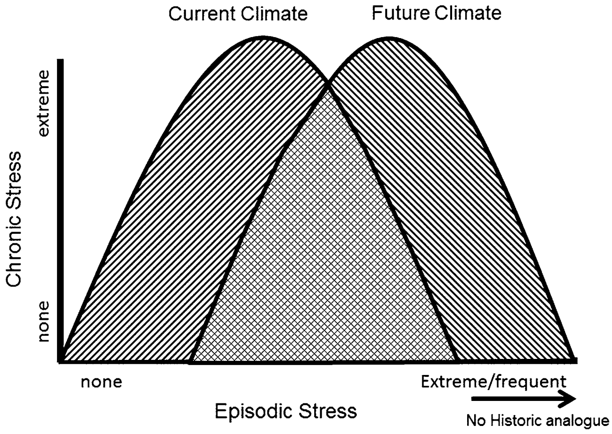


Fig. 3 Potential future relationship between ecosystem stress and forest mortality CS and NCS forest conditions

Fig. 4 Shift in episodic stress occurrence from current conditions



episodic stress becomes common. These limited resource trees may be less susceptible to increasingly common synergistic disturbance events and weather variability, but they will also be less productive in a traditional forestry sense. Conversely, NCS trees will likely continue to outperform CS trees regarding growth on an annual basis, but the risk of catastrophic mortality among these faster growing trees should also be considered within the rotation length and management of a stand.

Implications for forest genetics and silviculture

Over the past several decades, forest geneticists have made substantial advances in breeding for increased forest productivity, quality and disturbance resistance (Sutton 2002; White et al. 2007). Nothing in our hypothesis suggests the research to further improve individual tree performance should be altered. For example, hurricane intensity and frequency are expected to increase (Knutson and Tuleya 2007). Increasing the density of wood is one of the goals of genetic research (Zobel and Jett 1995). While a primary objective of genetic research may be to increase wood quality, an increase in wood density also reduces tree susceptibility to high wind damage (Curran et al. 2008). However, an increase in wood density would not assist with tree resilience to drought, which could to be a primary stress in future forests (IPCC 2007).

Genetic research focused on increasing tree growth rates should continue to be a priority despite the increasingly complex interactions with climate change and variability. There are well established relationships between increasing atmospheric CO_2 and tree growth (Oren et al. 2001; Norby et al. 2006). However, nutrient limitations may reduce or eliminate potential elevated atmospheric CO_2 fertilization impacts (Oren et al. 2001). Finzi et al. (2006) found that increasing nitrogen availability (but not nitrogen use efficiency) significantly increased forest growth under conditions of elevated atmospheric CO_2. Therefore, genetic advances designed to increase root nutrient (and water) uptake could significantly increase forest growth while maintaining water acquisition capacity during drought. Some researchers are actively examining ways to improve drought hardiness of trees on poor quality sites (Dvorak 2012). These studies are designed to increase the resistance of trees to drought related mortality. However, the studies are being conducted under current and historic climatic conditions. This paper raises the central question of whether or not the trends in tree and ecosystem response to historic chronic and episodic stress will persist as climate variability and stress become more extreme.

Forest management may be useful in reducing ecosystem stress while maintaining high quality forests. In the case study presented in this paper, increased leaf area may be a primary cause of ecosystem stress through both tree desiccation and increased success of southern pine beetle colonization. If individual tree leaf area (and tree growth) is to be maintained, then stand level leaf area should be reduced through reduced initial stand stocking, increased control of ground vegetation, and through more aggressive pre-commercial and commercial thinning. These control measures can significantly reduce tree evapotranspiration and therefore better conserve soil water during times of drought stress (Brix and Mitchell 1986). However, forest management such as thinning may also be needed to restrain maximum potential forest growth so that a “resource availability buffer” can be created as a hedge against extreme climatic conditions and associated secondary impacts (e.g., increased insect, disease, or wildfire risk). The choice to harvest more water demanding tree species (e.g., sweetgum) during harvest or to encourage more fire or drought tolerant tree species during forest regeneration [e.g., long-leaf pine (*Pinus palustris*)] are additional management practices that could be used to maintain a more resilient forest. Increasing tree volume growth is one of the primary objectives for pine plantation genetic improvement. However, under a changing and more extreme climate, faster growth rates will likely be associated with increased leaf area (McDowell et al. 2007). In turn, increased leaf area is associated with tree increased water use, and increased water use can lead to increased ecosystem water stress (Sun et al. 2011). Therefore, forest managers may want to reduce the demand on the water resources base by maintaining forest stocking level below what would be considered optimal for timber production through heavier, more frequent thinning. A more open forest will mimic the conditions observed in recent low tree mortality CS sites with regards to buffering against episodic, catastrophic disturbance. However, applying this practice in a NCS forest will maintain individual growth productivity at a higher rate than in a CS forest.

Unfortunately, heavy thinning has other side-effects. The more open canopy, and relative increase in water and nutrients will encourage understory and unwanted species regeneration (Alaback and Herman 1988; Aukema and Carey 2008). If left to accumulate, the increased understory vegetation will increase soil water use, increase crown fire risk

(Keyes and O'Hara 2002), and nullify the purpose of the thinning (i.e., to reduce resource stress). Increased solar radiation deeper into the crown can also cause increased epicormic branching and reduced tree lumber value (Pelkki 1999). Finally, both the cost of thinning (including pre-commercial thinning) and loss of overall stand productivity should be weighed against the potential for catastrophic mortality. If climate change is altering the dynamics of natural forests, climate change would likely also be altering the dynamics of plantation forestry. If so, then geneticists and forest managers need to work together to reduce forest mortality while maintaining overall forest productivity.

Conclusions

The long-lived nature of green-house gases such as CO_2 suggest that the impacts of climate change will be present for many decades to come (IPCC 2007). As the Earth continues to warm, and extreme climatic events become more frequent, extreme impacts from these events are also becoming more common. In addition to extreme episodic events, chronic, multiple stress impacts are also on the rise (Karl and Melillo 2009). The occurrences of extreme disturbance combinations are providing new insight regarding ecosystem response to environmental stress that have been rare in recorded history. Historically, NCS trees have better survived episodic stress compared to CS trees. However, eposodic stress may kill some individuals, and therefore free up resources to surviving individuals as a episodic stress continues or intensifies. CS stands may be more likely to lose individuals due to low level episodic stress, and therefore may be better situated to survive extreme secondary or interactive episodic stress impacts. While this situation is currently a rare occurrence, it may become more common in the future.

Both forest genetics and management can be useful in replicating the conditions that would increase forest resiliency to stress and disturbance while maintaining forest value. The case study used to develop the hypothesis of *the Rise of the Mediocre Forest* is currently an anomaly. However, climate forecast models project that the conditions needed to create points of inverse risk between CS and NCS trees may become more common in the years and decade to come (Fig. 4). Kosiba et al. (2013) found that New England red spruce trees, which during the 1980s–1990s had been in decline, are now inexplicably growing at record rates. Kosiba et al. (2013) were perplexed as no specific change in growth conditions were found to account for the changing growth pattern. Perhaps the previous decades of tree mortality may have increased current resource availability and were at least partially responsible for the current growth increases across the region. Based on the reasoning proposed in this paper, we would hypothesize that the New England red spruce growth gains could be short lived (1–2 decades) and ultimately result in catastrophic mortality across the region at a point when the resources are fully utilized, the forest has acclimated to a new more resource demanding state, and a severe episodic stress (e.g., drought, heat, insects) occurs. If this scenario is correct, then forest managers will need to develop and apply new silvicultural practices to reduce mortality in traditionally healthy forests or risk the establishment of a new paradigm in the forest condition where periods of rapid growth are followed by a short but intense period of forest mortality. Regardless of how common or how severe future stress and disturbances become, forest science will need play a prominent role in adapting to these changes.

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