CLIMATE CHANGE AND AUTUMN COLORS In New England's Forests

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ABSTRACT

This paper reviews the process of leaf color change in the deciduous forests of New England and the possible consequences of climate change on color change events. Implications of a changing fall color regime on regional fall tourism are also examined. Around the globe, it is well recorded that earlier spring events are strongly correlated with rising temperatures, but the influence of climate change on the timing of autumn events is less well understood. Autumn senescence is the phenomenon in which deciduous trees lose their leaves, a period during which many species undergo a brilliant fall color display. The primary trigger of autumnal color is the shortening photoperiod, but other environmental factors may influence the quality of the color display. The primary environmental influences on the quality of the fall foliage display include temperature, sunlight, and moisture. Because changes in these environmental factors are linked with ongoing climate change, the future of fall color displays may be adversely affected. The current most pressing risks to the color displays in the forests of New England are severe weather events and climate-induced shifts in species distributions. As a result of actual or even perceived change, fall color tourism markets are expected to suffer. Keywords: autumn coloration, global climate change, fall foliage, tourism, New England.

Introduction

In the northeastern United States, the change of seasons is marked each year by the leaves changing colors in which the green leaves of summertime fade into brilliant shades of yellow, orange and red before falling from the trees. It widely accepted that environmental factors such as light, moisture and temperature influence the duration and intensity of autumnal leaf coloration (Addicott 1968). Fall foliage can be seen in many temperate regions of the world, but the forests of New England are especially well-known for their vivid fall color displays. There are many different tree species in the forests of New England, but only some of them produce colorful autumn foliage (Table 1). The most well-known of these trees is the sugar maple (*Acer saccharum*

Marsh.), which is common throughout the northeastern United States.

Until recently, the multiple interrelated environmental factors influencing autumn colors had not been rigorously studied and research was limited to observation-based knowledge. Autumnal leaf events have long been a fascination of humans, and records from ancient Greece indicate an early awareness of the relationship between environmental factors and leaf color change. Greek botanist Theophrastus noted that good soil "and a moist situation conduce to keeping the leaves late; for those which grow in dry places, and in general where the soil is light, shed their leaves earlier, and the older trees earlier than the younger ones" (Addicott 1968, 1471). The accumulation of observations from hundreds of years of leaf change has helped in making predictions of the timing of autumn color change events but fully understanding the principal mechanisms behind these changes has been more difficult.

It is now understood that phenologic events (i.e. climate-sensitive periodic biological phenomena such as flowering, budding, and leaf fall) have been shifting as a consequence of climate change (Matsumoto et al. 2003; Ibáñez et al. 2010). These shifts are important pieces of evidence for the possible ecological consequences of climate change.

Regardless of the reason for leaf color change, forests of the northeastern United States change colors in autumn and humans enjoy watching the spectacular event. The changing colors of autumn leaves are an ephemeral phenomenon but commonly last for up to two months depending on geographic and interannual climate variation (Archetti and Leather 2005). The future of the economic welfare of the region is closely tied to this natural event, especially in the tourism sector. During the fall season, the New England region brings in \$8 billion annually to local revenues (USDA 2011a).

This essay reviews the current body of knowledge on autumnal leaf events, how climate change may influence the onset, duration or intensity of autumn coloration in New England forests, and how potential climate changes may, in turn, influence regional tourism related to fall color change.

Why do leaves change color? Biochemistry of Fall Color

Autumn leaf senescence, a type of programmed cell death, is triggered by the shortening day length in autumn (Keskitalo et al. 2005). The mechanisms within the leaves that control fall coloration in trees primarily involve three groups of plant pigments: chlorophylls, which absorb blue and red portions of the visible light spectrum and reflect green; carotenoids, which reflect red, yellow, and orange light; and anthocyanins which reflect red, blue, and indigo (Coder 2008a). Multiple color combinations are possible with the fading, unmasking, and generation of the different leaf pigments.

In a study on the autumn senescence of free-growing European aspen (*Populus tremula* L.) in east-central Sweden (Umeå University) during one season, Keskitalo et al. (2005) compiled measurements of pigments and important metabolites within the leaves throughout the autumn senescence period to create a generalized cellular timetable of the entire process. Green sum-

Scientific name	Common name	Predominant color
Acer rubrum L.	red maple	Red and purple
Acer saccharinum L.	silver maple	Yellow, brown
Acer saccharum Marsh.	sugar maple	Yellow-orange to red
Alnus spp.	alders	Little to no color
Betula spp.	birches	Yellow to orange
Carya spp.	hickories	Yellow to orange
Fagus grandifolia Ehrh.	American beech	Yellow, orange, bronze
Fraxinus spp.	ashes	Yellow, orange, red
Ginkgo biloba L.	ginkgo	Yellow to orange
Liriodendron tulipifera L.	tuliptree	Yellow to orange
Prunus serotina Ehrh.	black cherry	Yellow, red
Populus spp.	poplars	Little to no color
Quercus alba L.	white oak	Yellow to orange, red
Quercus rubra L.	northern red oak	Red and purple
Sassafras albidum (Nutt.) Nees	sassafras	Yellow, orange, purple
Tilia americana L.	American basswood	Dull green to yellow
Ulmus spp.	elms	Dull green to yellow

Table 1. Tree species of New England and their typical fall colors. Adapted from Clatterbuck (1999) and CT DEEP (2012a).

mer leaves contain both chlorophyll and carotenoids, while anthocyanins are only produced in certain tree species during mid-senescence. The carotenoids, which are present in the leaf throughout the year, are revealed as chlorophyll begins to break down in the leaf. As the photoperiod decreases due to shorter daylengths and lower sun angles, chlorophyll production slows and eventually ceases, existing chloroplasts begin to degrade within the leaf, and the rate of photosynthesis declines (Keskitalo et al. 2005.). This degradation phase reveals carotenoids and other pigments that had been present in the leaf but masked by chlorophyll during the growing season. Eventually, a protective abscission layer is formed on the stem of the leaf. During

leaf senescence processes, nitrogen, phosphorous, and sulfur are pulled from the leaves to twigs and branches for winter storage before abscission. With nutrient deficiencies in the leaf, certain species synthesize anthocyanin pigments (Schaberg et al. 2003). Furthermore, low temperatures and the developing abscission layer slow sugar flow from the leaf. The sugars react with anthocyanidins, promoting anthocyanin production (Koike 2004). As the cell walls of the abscission layer become dehydrated, the leaf loosens and falls. Keskitalo et al.'s (2005) timetable suggests that once the pathway for senescence has been initiated by a shortening photoperiod, environmental factors, such as light and temperature, have little effect on the duration of the process.

Evolution of Fall Color

In temperate regions, deciduous tree species undergo the process of abscission, i.e. the annual shedding of their leaves. Unlike coniferous species, the leaf tissues of deciduous trees typically cannot survive winter frost, and are sealed off from the rest of the tree and fall off to ensure the tree's survival through the cold and dry conditions of winter. Much is known about the biochemistry and physiology of leaf senescence, but despite advances in the current body of knowledge surrounding autumn senescence, the adaptive value of autumn coloration (especially of red coloration) remains somewhat of a mystery (Archetti et al. 2008; Ramírez et al. 2008). Until recently, autumn colors have been dismissed within the scientific community as a mere by-product of leaf senescence. But now this notion is generally considered incorrect and several hypotheses have been developed to explain the evolution of fall colors (Archetti et al. 2008).

Brilliant autumn color displays are an exception among deciduous tree species since the majority of species do not exhibit colorful leaves in autumn. In a study of 2,369 temperate tree species, Archetti (2009) found that red autumn colors were present in at least 290 species of 70 genera (~12 percent of deciduous species), and yellow autumn colors were present in at least 378 species of 97 genera (~16 percent of deciduous species). Archetti's study suggests that fall leaf coloration has evolved independently multiple times, making it more difficult to directly discern the adaptive value of this trait.

Carotenoid pigments are present in the leaf year-round, and function primarily to absorb light energy and to protect chlorophyll from photodamage (Armstrong and Hearst 1996). However, since red (anthocyanin) coloration is produced exclusively in autumn, it cannot be a mere by-product of senescence. There are currently two main hypotheses concerning why trees produce red coloration in autumn and how this trait evolved. The first hypothesis is that red coloration has adaptive value in that the red pigments protect the leaves against harmful effects of light at low temperatures in autumn (Hoch et al. 2001; Feild et al. 2001; van den Berg et al. 2009). In cold weather and under intense light conditions, the efficiency of photosynthesis declines (Ramírez et al. 2008). The presence of anthocyanins filters out ultraviolet light and protects surrounding tissues and chloroplasts from ultraviolet radiation damage, which allows photosynthesis to continue longer into the autumn season and allows trees to build greater sugar reserves before the photosynthetically unproductive winter (Ramírez et al. 2008). Anthocyanins also protect against leaf damage by absorbing free radicals and conserving leaf water, which provides some protection against frost damage (Coder 2008a).

The second hypothesis is that red coloration emerged out of coevolutionary interactions with insects (Archetti et al. 2008). According to this hypothesis, red leaves act as a warning sign of a tree's defense level to insects (Ramírez et al. 2008). Healthier trees are able to produce more anthocyanins, which in turn deters egg-laying insects in search of a host for their offspring. It has also been proposed that autumn coloration acts as a signaling function for other animal species in the forest ecosystem. Lev-Yadun and Gould (2007) suggest five potential interactions: (1) to signal the presence of ripe fruit to enhance seed dispersal by frugivores; (2) to signal tree health and defensive ability to deter aphids; (3) to undermine the camouflage ability of herbivorous insects; (4) to indicate chemical defense by red coloration; or (5) to indicate leaf nutritive value to herbivores. None of these alternative hypotheses for anthocyanin production is universally applicable to all coloring tree species and there is a general lack of supporting experimental evidence (Archetti et al. 2008).

Environmental Influences on Color Change

Day Length and Light Intensity

The sequence of events in autumn coloration is primarily triggered by the shortening day length. Short days and long nights induce the beginning stages of autumn coloration before leaf abscission (Koike 2004). Bright, cold days are known to intensify anthocyanin color production but the physiological basis of light intensity is not well understood (Lee et al. 2003; Keskitalo et al. 2005). The amount of anthocyanins produced in the leaf, and therefore the intensity of red and purple coloration, depends on the amount of sunlight during the autumn season, unlike carotenoids which are present year-round. As a result, yellow coloration is much more consistent than red coloration from year to year (USDA Forest Service 2011b).

Keskitalo et al. (2005) found that the accumulation of anthocyanin in European aspen leaves fluctuated based on the amount of sunlight. The effect of sunlight on anthocyanin production is often seen in maple species (*Acer* spp.) as the crown of the tree, which is exposed to more sunlight, turns red before the lower leaves. Lee et al. (2003) found that by shading red-senescing leaves from sunlight, both chlorophyll degradation and anthocyanin production were suppressed. These studies suggest that the shortening photoperiod, which is not influenced by climate change, signals the onset of fall coloration. Changes in cloud cover and precipitation patterns can influence light intensity, thereby influencing the vividness or brilliance of the fall color display. However, once coloration phases are triggered, the amount of sunny or cloudy days may not influence the length of the color season.

Temperature

Studies have shown a strong correlation between temperature and the timing of the onset of spring phenological events (Zhou et al. 2001; Root et al. 2003; Taylor et al. 2008). The influence of temperature on the timing of autumn events is less clear. Some studies have suggested that autumnal events occur later in warmer years, while others have suggested that temperature

does not influence the onset of fall color (Lee et al. 2003; Ibáñez et al. 2010). Trends that relate the timing of autumn events solely to temperature show a great deal of variation, suggesting that an individual tree's response to temperature is complex and that the influence of temperature is interacting with other environmental conditions such as soil moisture or nutrient levels (Ibáñez et al. 2010).

The relationship between temperature and color intensity is better understood, and a specific balance of daytime and nighttime temperatures is necessary for vivid fall color displays. As a general rule, it can be expected that trees produce the most visually spectacular fall color displays when there is a 5° to 7°C difference between daytime and nighttime temperatures (Koike 2004). The crisp nights and bright, sunny days during a New England autumn promote vivid leaf coloration. The warm days promote photosynthesis to continue but the cold nights prevent the resulting sugar to flow from the leaf downward the tree, resulting in anthocyanin production in the leaves (CT DEEP 2012b). A warm period during the fall can result in warmer nights and dull autumn colors (USDA Forest Service 2011b). Additionally, an early frost can damage the cellular machinery responsible for anthocyanin production and shorten the color season (Coder 2008b).

Moisture

Precipitation and soil moisture greatly influence the quality of autumn color expression. A growing season with ample moisture followed by a dry autumn results in maximal color development (Koike 2004). Leaf abscission usually occurs once there is an insufficient level of soil moisture (Escudero and del Arco 1987). Therefore, overly dry conditions can cause the abscission layer to form prematurely and cause the leaves to drop before fully developing their fall color displays.

Other Environmental Influences

Additional environmental factors may also influence autumn leaf colors, including soil nutrients and soil composition (Escudero and del Arco 1987). Low soil fertility may prolong leaf retention (Koike 2004). Mild drought stress in autumn can enhance anthocyanin production (Coder 2008b). Stress during a growing season leads to lower nitrogen levels and greater accumulation of sugars in the leaves. High sugar content triggers anthocyanin production, resulting in more vivid red hues (Schaberg et al. 2003). More severe stresses, however, can diminish leaf longevity.

Color Change and Climate Change

Current Observations of Change

It is evident that local variations in climate have a strong influence on the progression of fall color. The most vivid fall color requires a perfect combination of light, temperature, and

moisture conditions. Interannual, interspecies, and individual variation in fall color is expected, but human-influenced climate change adds another layer of complexity to this already complex phenomenon. Observational data collected in New England indicate that, compared to twenty years ago, sugar maples in the Hubbard Brook Experimental Forest (New Hampshire) reach dormancy two to five days later and leaves in the Harvard Forest (Massachusetts) begin to change color three days earlier (Sharp 2011). Although leaves begin to change colors earlier at the Harvard Forest, there has been very little change in the date of 50 percent leaf loss over an eight year period (Lee et al. 2003). Public observations throughout New England of foliage color and leaf drop recorded by The Foliage Network (2013) during the period 1999-2011 indicate that the onset of coloration begins later in September and that the duration from coloration to leaf drop appears to be decreasing (Figure 1). However more years of observation are necessary to detect any definitive trends in timing and duration.

The forests of New England may be more susceptible to climate-induced changes in fall coloration than forests in other regions. According to historical records, the average air temperature in the northeastern United States has increased 1°C over the last century, while the global average temperature has only increased 0.75°C (Rustad et al. 2009). Shifts in important climate indicators, such as spring bud-break or the first frost, have been well documented in the northeastern United States (Wolfe et al. 2005; Richardson et al. 2006; CT DEEP 2009; Burns et al. 2010). Hayhoe et al. (2007) studied past records and used atmosphere-ocean general circulation models to predict future changes in key climatic, hydrological, and biophysical indicators in the Northeast. Many of the environmental factors thought to influence the timing, duration and intensity of fall coloration (e.g. temperature, precipitation, drought frequency) are predicted to change significantly in the coming century (Hayhoe et al. 2007).

Light Intensity

Although day length will not change with global climate change, the intensity and availability of daylight can be affected by changes in cloud cover. Increased cloud cover and the resulting decrease in available light during a growing season reduces photosynthesis. Less photosynthesis, relative to respiration, lowers sugar reserves and, consequently, lowers the production of anthocyanins (Schaberg et al. 2003). The decreased light availability due to cloud cover can therefore yield muted fall colors.

Studies suggest that an increase in light availability due to light pollution can play a significant role in leaf retention (Holker et al. 2010). Trees growing within 45 feet from New York City streetlamps retained their leaves up to one month beyond the normal season for nonilluminated trees (Matzke 1936). Since the trees were compared to other nearby street trees, temperature increases associated with an urban heat island effect did not induce the reported differences. For trees in remote, natural forests, light pollution is less problematic, but it is possible that forests in urban, suburban, and exurban environments could be affected by light pollution. Increased housing density due to accelerated population growth in much of rural, non-metropolitan New England may lead to increased nighttime lighting (Nowack and Walton 2005; Stein et al. 2005; Johnson 2008). Even small amounts of light could disrupt natural pho-





toperiod responses and possibly lengthen the duration of the autumn color viewing season.

Temperature

Mean global temperatures are becoming warmer. Likewise, mean annual temperatures in New England have increased an average of 0.26°C per year over the past thirty years (Spanger-Siegfried 2006). The region is projected to be warmer (2-6°C increase over the next century) and wetter by the end of the century compared to the 1971-2000 baseline (Spanger-Siegfried 2006; Tang et al. 2012). Many studies have shown that while environmental factors like temperature influence the intensity of fall color displays, they are not influential on the timing of the onset of autumn senescence (Lee et al. 2003; Keskitalo et al. 2005). Conversely, long-term studies (fifty years) in Japan and South Korea report a correlation between warmer air temperatures and delayed foliage coloration (Matsumoto et al. 2003; Ibáñez et al. 2010). Similarly, based on modeling of three temperate deciduous tree species, Delpierre et al. (2009) predict that by the end of the century the onset of autumn coloration will shift one to two days later per decade in France, primarily due to rising temperatures. In a single species, autumn senescence can vary greatly across its geographic range (Morin et al. 2009). As the climate warms, patterns of autumn coloration may have the capacity to shift in latitude relative to rising temperatures.

If climate change results in warmer autumn daytime and/or nighttime temperatures in the New England region, onset of peak fall colors may be delayed one to three weeks. With warmer temperatures, the growing season will be prolonged and possibly displace the timing of leaf fall due to the disconnect between a shortening photoperiod and cooling temperatures. A prolonged growing season can mute color displays due to lower rates of photosynthesis during the autumn's shorter daylight hours. Lower rates of photosynthesis lead to less anthocyanin production and less vibrant displays of red coloration.

If portions of New England experience cooling trends with global climate change, the cooling autumn temperatures might remain in synchrony with the photoperiod. If such is the case, timing may not be significantly altered. Cooler nighttime temperatures can cause stress to the trees, resulting in more vivid reds due to increased anthocyanin production. Early frosts can cause leaf fall to occur earlier, possibly before coloration can occur, thereby shortening the duration of the fall color season.

Precipitation

While precipitation trends are more difficult to assess than observed historical changes in temperature due to interannual variability, it is apparent that precipitation has been increasing in the northeastern United States (Huntington et al. 2009; Tang et al. 2012). Even if the total amount of annual precipitation remains relatively stable, there have been observed pronounced shifts in the seasonal distribution of rainfall in which the northeastern United States has experienced a relative increase in winter precipitation and a decrease in summer precipitation since the 1970s (Hayhoe et al. 2007). Additionally, the frequency of intense precipitation events (≥ 2

inches of rainfall within 24 hours) has increased in the past thirty years (Douglas and Fairbank 2011). Autumn leaves are vulnerable to early abscission during these weather events because of the physical energy of heavy storms on weakly attached leaves.

Huntington et al. (2009) suggest that not only will rainfall become more intense, but large storms will become more frequent with longer intervening dry periods. Drought-stressed leaves might display more vivid red colors (due to nutrient stress) but tend to drop prematurely due to a dry, fragile abscission layer. Trees might not display coloration before leaf fall. As a result of changes in the strength and distribution patterns of precipitation, the overall leaf fall season is expected to end earlier due to intense storm and drought events.

Other Environmental Influences

Human activity has increased the concentrations of pollutants in the air, especially that of the greenhouse gas carbon dioxide (CO_2) . While rising CO_2 levels are associated with rising global temperatures, the increased CO_2 itself can play a role in patterns of phenological events. Various studies of deciduous trees in temperate environments have suggested that CO_2 enrichment of the atmosphere will increase net primary productivity of most tree species (Norby et al. 2003; Ollinger et al. 2007; Lindroth 2010). Although increased CO_2 can promote plant productivity, it has not been shown that the elevated CO_2 itself has any predictable effect on the timing of autumnal events (Norby et al. 2003). However, the increase in productivity results in less stress during the growing season which may lead to less anthocyanin production and less red coloration (Schaberg et al. 2003). Other air pollutants associated with human activity, including tropospheric ozone and acid precipitation, can cause stress to trees and cancel out any gains in productivity from enhanced CO_2 (Kubiske et al. 2006).

Productivity can also be compromised by forest pests and pathogens. Changes in winter freeze-thaw cycles have increased the occurrence of tree pest and pathogen outbreaks and are associated with die-backs of several hardwood species of the northeastern United States (New Hampshire Department of Environmental Services [NHDES] 2008). Introduced pests have the capacity to influence shifts in tree species distributions. Significant introductions that have changed the forest composition and structure of northeastern forests include the gypsy moth as well as the fungi associated with Dutch elm disease and chestnut blight (Yahner 1995; Dodds and Orwig 2011). Current threats to deciduous trees in New England forests include beech bark disease, emerald ash borer, European winter moth, and Asian longhorned beetle.

Trees species that become threatened by pathogens and pests are often replaced by other more competitive dominant tree species (Yahner 1995). As a result, forest structure and function has the potential to change drastically and in a relatively short period of time. For example, maple species were the preferred host of Asian longhorned beetles in maple-dominated natural hardwood forest stands near Worcester, Massachusetts (Dodds and Orwig 2011). Eradication of maple species in an effort to stop the outbreak led to an oak-hickory dominated forest stand (Dodds and Orwig 2011). The change in species dominance may result in a change of edaphic conditions due to the loss of the easily decomposed, calcium-rich maple leaves from the forest floor.

Multiple disease risk hotspots are located throughout the northeastern United States. Some areas currently valued for fall foliage viewing (e.g. White Mountain National Forest, central Vermont, central Adirondacks) may experience greater than 25 percent tree mortality by 2020 due to insects and disease (USDA Forest Service 2007). Tree mortality from pests and pathogens combined with drought events could lead to further large-scale tree mortalities due to wildfires.

Shifts in Forest Composition

Species distributions in the forests of the northeastern United States are certainly not static and have been shifting for thousands of years (Shuman et al. 2004). As glaciers retreated northward at the end of the last ice age, tundra-like vegetation inhabited much of New England with open spruce (*Picea* spp.) woodlands in southern portions of the region (Bonnicksen 2000; Shuman et al. 2004). Early forests of red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), and quaking aspen (*Populus tremuloides* Michx.) developed with warming temperatures following deglaciation approximately 14,600 years ago (Estrin and Johnson 2002). Changing temperature and moisture regimes led to continuous shifts in forest composition and tree species dominance (Shuman et al. 2004).

Humans first began to influence northeastern forests when Native Americans managed the landscape through fires and forest clearings (Harvard Forest 2011). Fires set by Native Americans may have discriminatively affected tree distributions by favoring fire-tolerant species, such as oaks (*Quercus* spp.) (Yahner 1995). At the arrival of European settlers, New England forests consisted primarily of mixed conifer and northern hardwoods with eastern white pine (*Pinus strobus* L.), American beech (*Fagus grandifolia* Ehrh.), maple (*Acer* spp.), and eastern hemlock (*Tsuga canadensis* (L.) Carrièr) being the most abundant species (Yahner 1995). Forest clearing in New England peaked between 1830 and 1850. During this time period, 60-80 percent of the land was cleared for agriculture and settlement (Harvard Forest 2011). As agricultural production in the United States shifted westward, abandoned New England agricultural lands reforested within several decades (Harvard Forest 2011). Abandoned pastures and fields most often reverted to pine forests, where dense understories of deciduous hardwoods, such as maple, flourished (Yahner 1995).

Today, human-accelerated climate change and its side effects are important drivers of species range shifts. In New England, tree species have shifted to higher elevations and, in some cases, higher latitudes in the past 50 years (Beckage et al. 2008; Tang et al. 2012). Additionally, future projections strongly suggest that the rate of migration will accelerate in the future (Morin et al. 2008). Tree species with narrow geographic distributions are most threatened by changes in climate (Morin et al. 2008). Maple-beech-birch forests (colorful fall foliage) are predicted to be displaced by the less colorful oak-hickory forests as the dominant forest type in the New England region (Figure 2) (Iverson and Presad 2001; Tang et al. 2012).



Figure 2. (A) Generalized forest cover types of New England in 2002-2003 from the U.S. Forest Service Forest Type Groups (Northeast US) data set (USDA Forest Service Forest Inventory and Analysis Program and Remote Sensing Application Center). (B) Predicted forest cover types for New England in 2071–2099 under IPCC (International Panel on Climate Change) SRES (Special Report on Emission Scenarios) climate scenario A1B, based on Tang et al. (2012).

Color Change and Society

Economic Impact

In New England, climate change is predicted to negatively affect certain niche economic sectors. For example, snow-based recreation is expected to suffer due to shorter seasons and increased artificial snowmaking (Dawson et al. 2009). Recreational fishing may suffer from thermal stream degradation causing a loss of suitable habitat for cold-water fish and reduced water levels and flow rates due to an increase in droughts (Bloomfield 1997). Warm nighttime

temperatures in the spring will reduce the number of optimal sap flow days thereby negatively affecting the maple syrup industry (Skinner et al. 2010). Shifts from maple forests to oak forests will reduce the abundance of sugar maples available to tap in the region.

The fall foliage tourism season is most vulnerable to climate change through the quality of the color display. Dull fall foliage may seem to be one of the least significant consequences of climate change and may appear superficial when compared to more severe consequences that threaten human economic welfare, such as sea level rise or crop failures. But many people in New England rely on the income that fall color tourism provides. Fall color tourism, also known as leaf-peeping, is a niche-market that is of significant economic value to the forested areas in the northeastern United States. The color tourism season usually lasts nearly two months (September to mid-November), with colors peaking for roughly three weeks in mid to late October depending on the region (USDA Forest Service 2011b). Autumn tourism is especially successful in New England because of the close proximity between the expansive deciduous forests and highly populated areas along the East Coast. New England states, with the exception of Rhode Island, maintain state-sponsored websites actively promoting fall foliage tourism with current foliage reports and hotlines.

The autumn tourism industry in New England generates \$8 billion annually (USDA 2011a). In Vermont, fall color tourism brought in 3.6 million visitors and \$332 million in 2009 and accounts for 22 percent of the state's tourism market (Graham 2011). Forty percent of Connecticut's tourism revenues are due to the 4 million fall foliage visitors (Salzman 2005). Maine and New Hampshire drew 8.6 and 8 million visitors, respectively, during the 2009 fall foliage season and \$2.6 billion combined (Kane 2010). In contrast, the 2009-2010 winter ski season attracted 4.1 million visitors and \$750 million to Vermont and snow-based recreation generates approximately \$650 million in visitor spending annually in New Hampshire and 13.5 million skiers generating \$4.6 billion (all snow sports except snowmobiling) annually to the New England region (Frumhoff et al. 2007; Dawson et al. 2009; Edelstein 2010).

From an initial survey of nationally representative households, Brown (2002) surveyed households that responded affirmative to visiting or planning to visit Vermont in order to profile fall foliage tourism in Vermont. Viewing fall foliage was the top reported primary purpose for visiting Vermont in the fall of 2001. Seventy percent of the fall color tourism spending affected three financial sectors: lodging, retail, and restaurants (Brown 2002). Fall foliage visitors were more likely to buy Vermont-made products (44 percent bought products) than visitors not participating in fall color viewing (7.6 percent bought products) (Brown 2002). In New Hampshire, fall color tourists spent 16 percent more than their non-fall color viewing counterparts (NHDES 2008). Despite the lack of thorough studies assessing fall foliage visitation rates and expenditures per state in the northeastern United States, it is evident that a considerable share of the New England tourist industry is linked to fall color viewing. A network of lodging, dining, and retail businesses thrives and depends on fall foliage tourism. As the timing of peak coloration and quality of foliage displays changes due to changes in climate and in species composition, the fall foliage industry of New England will have to adapt in order to synchronize fall festivals and peak visitation with peak foliage conditions (Wilmot 2011).

Regardless of an actual effect of climate change on the timing, duration, and intensity of fall

foliage, there is the problem of public perception. In one news report, a plant biologist from the University of Vermont notes that leaves have not developed brilliant color displays in recent years, while a representative from the state tourism office rejects this notion as a problem of perception tinged by nostalgia (Gram 2007). Both of the individuals clearly have a biased view of the subject and even so, prospective tourists are apt to be influenced negatively. Following the Deepwater Horizon oil spill in the Gulf of Mexico, tourism in the southeast experienced a strong decline (Padgett 2010). Although oil was not predicted to reach many southern Florida beaches, concerned tourists cancelled existing reservations and the tourism industry suffered. False impressions of an ecological disaster dissuaded many people from taking the chance of a spoiled beach vacation. Similarly, the thought of a dull or unpredictable fall color season could threaten the tourism industry of New England. Even if climate change does not have a significant negative effect on the timing, duration or intensity of fall coloration, people may be more reluctant to visit the region in the future.

Conclusions

Due to interannual, interspecies, and individual variability in color production, it is difficult to predict the timing, duration, and coloration of fall foliage. However, observations in research forests of New England indicate that fall color events are shifting and these shifts may eventually reveal trends related to climate change (Zhang et al. 2012). Although our review is specific to fall foliage in New England, it has implications for understanding the effect of climate change on fall foliage events across the world's temperate regions. Shorter durations from initiation of coloration to leaf drop are expected due to prolonged growing seasons which delay the onset of coloration and an increasing risk of intense storms or severe droughts which cause leaves to drop prematurely, possibly before leaf colors have fully developed. The intensity of fall foliage coloration, specifically through the production of anthocyanin, is expected to become more vivid with mild stresses like drought-stress or nutrient-stress with a shifting precipitation regime or from photochemical leaf damage during a growing season due to tropospheric ozone and acid deposition. Conversely, muted colors are expected with an increase in forest productivity with increased atmospheric CO_2 levels, with warmer nighttime temperatures, with increased cloud cover, or with shifts in species dominance due to pest and pathogen outbreaks.

An important indirect effect of climate change on New England's fall colors is the shift in the distribution and composition of forest types with changing temperature and moisture regimes. The sugar maples and other northern hardwoods known for the most brilliant colors in the northeastern United States may migrate 100 to 300 miles north to be replaced with species that now grow to the south and in lower elevations like oaks and southern pines and display less vivid or no fall coloration (NHDES 2008). Dulling fall foliage should not be dismissed as a superficial consequence of climate change as it supports a significant regional tourism industry. Furthermore, changing patterns in the timing and duration of fall foliage events are useful environmental indicators of biophysical alterations of important ecosystem services such as water quality, air quality, or erosion control.

Autumn colors, especially those in New England, are a wonderfully scenic natural phenomenon. Climate change has the potential to dramatically affect New England as a fall tourist destination, which may have significant economic implications for some regions. Gaps in the literature exist both regionally for New England and for temperate regions worldwide regarding the influence of climate change on fall foliage events and in fall foliage tourism research. Longterm studies of past color events are necessary to establish any relationships between fall foliage events and recorded climatic factors. Existing and future literature documenting these relationships should be modeled in order to project changes in timing, duration, and intensity based on different climate change scenarios. Data regarding fall tourism revenues need to be compiled throughout the New England region in order to quantify economic projections within the context of climate change. Actual or perceived changes in fall color intensity may have a significant impact on the future of the fall tourism market. Surveys of fall foliage tourists for the region are needed in order to determine if changes in timing, duration, or intensity of fall color events have a potential effect on tourist behavior.

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