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Brief Communication

Forest Ecology

Alternate Growth Forms Can Protect Climate-Threatened Trees from Freezing Stressors

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Abstract

Climate change creates a variety of novel stressors for species, such as a decline in snowpack. Loss of snow has many impacts, including the loss of thermal insulation of soils. Winter/spring freezing of soils has been tied to forest mass mortality in multiple locations around the world. Many species, however, can take alternative growth forms, such as tall tree forms and short shrub-like forms. Shrub-forms may provide a unique protection from the snow loss phenomenon by providing a similar thermal insulation as snowpack. That hypothesis is tested here using yellow-cedar, a species undergoing mass mortality due to snow loss. Temperature loggers were placed under both tree- and shrub-form cedars, including areas where the species was experimentally removed. The number of soil freezing days was high in open areas, areas of tree mortality, and where the shrub-form was removed, but was almost zero in areas where the shrub-form was left intact. This suggests that growth-form temperature moderation is possible and may provide an important resistance to the mortality mechanism. In other areas around the world where snow loss is resulting in soil freezing and mortality, growth forms should be investigated as a potential moderating mechanism for this particular climate change stress.

Study Implications: Many tree species are experiencing rapid die-off due to soil freezing, as snow declines and the ground is exposed to atmospheric temperature fluctuations. Although shrub-like growth forms of those same species are rarely investigated, the frutescent structure moderates soil temperatures, minimizing soil freezing events even in late spring when snow is gone. This provides an important refugial condition for species at risk and perhaps a way to navigate the transition from colder to warmer winters in the future while remaining a presence (albeit diminished) on the landscape.

Keywords: Climate change, snow, yellow-cedar, tree mortality, structure, growth form, morphology

Climate change–induced mortality is threatening forests around the world (Sommerfeld et al. 2018; Trumbore et al. 2015). Elevated mortality has been tied to altered frequencies or intensities of hot droughts (e.g., Hartmann et al. 2022), floods (Poff 2002), fire (Keeley et al. 2019), and many other mortality mechanisms.

One emerging challenge that has received relatively little attention is snow loss–induced mortality (beyond the impact of snowpack reductions on summer water stress). Snow loss in the winter can result in multiple challenges to trees, such as decreasing hydraulic capacity (Earles et al. 2018) or altered fungal pathogens (Senn 1999). Without the insulative snow layer, soil temperatures fluctuate with air temperatures, potentially leading to significantly colder soil (Groffman et al. 2001). Soil freezing and thawing, especially in locations where those events were historically rare, has significant impacts, including fine root injury (Zhu et al. 2000), changed bacterial and fungal dynamics (Sorensen et al. 2019), increasing mercury fluxes (Yang et al. 2019), increasing carbon and nitrogen losses (Matzner and Borken, 2008), and decreasing soil moisture (Hardy et al. 2001). Snow loss is expected to accelerate (Musselman et al. 2021), especially in areas where winter temperatures are already close to the freeze-thaw boundary (Buma et al. 2017; Meehl et al. 2004).

One underinvestigated aspect of species resistance to snow loss is morphological. Many species, such as *Salix* species, can take both a tree (“arboreal”) and shrub (“frutescent”) form. The frutescent growth form may be adaptive under stressful conditions, given its often relatively faster growth rate (e.g., basal area; Gotmark et al. 2016). In the context of snow loss, a change in structure leads to an interesting hypothesis: the frutescent form may function similar to the snowpack itself as an insulative layer that maintains higher soil temperatures in winter. Temperature moderation has been observed under krummholz growth forms associated with increased snow trapped around the individuals above tree line (e.g., Pyatt et al. 2016; Wardle 1968) but has been not tested in the context of snow loss and mass mortality, where it is not heightened collection but rather direct shading that may maintain snowpack longer in warming climate.

This study used yellow-cedar (*Callitropsis nootkatensis* D. Don), a well-known example of mortality associated with snow loss. The species is distributed from California to Alaska (USA). Winter warming and subsequent loss of snowpacks

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Figure 1. Typical scene. Mortality of the arboreal form is nearly complete (>90 percent basal area in many locations), but ample frutescent form individuals occur (arrow). Other trees are primarily Sitka spruce, western hemlock, and mountain hemlock. (Photo is approximately 100 m from the study site, chosen as it is easier to see the different forms with the open meadow. The study site is more sparse, allowing for discrimination between growth forms and treatments; see Methods).

over the last century is correlated with extensive mortality: 70% of basal area or more, across ~3,500 km^2 or 8% of the range (often termed "yellow-cedar decline," Buma et al. 2017). Tree death has been tied to late-season cold snaps and subsequent fine root mortality by both correlational and experimental studies (e.g., Hennon et al. 2012; Schaberg et al. 2008).

Yellow-cedar typically has a "standard," single-stemmed arboreal form, often reaching 40 + meters. Alternatively, it can take on a frutescent growth form, reproducing vegetatively via layering, which reaches a height of ~0.5 m, spreading laterally as a mostly continuous ground cover (Hennon et al. 2016). The frutescent form is rarely found in productive forests (likely due to light competition; Krapek and Buma 2018) but is common in low-slope *Sphagnum* bogs and fens where the snow loss–induced freezing mortality is most common (Buma et al. 2017). Interestingly, mortality from snow loss is typically seen only in the arboreal form of the species, despite being collocated and experiencing the same snow and air temperature regime (Hennon et al. 2016).

This study examined whether growth form can modulate the effect of snow loss by measuring soil freezing frequency during late season (post-snow) cold snaps.

Methods

The study location (latitude: 56.8494, longitude: −133.5261, elevation: 250 m) is near Kake, Alaska, centrally located in a snow loss–affected area of the species range (Buma et al. 2017). This site and region has been the subject of extensive research on yellow-cedar mortality impacts (e.g., Bisbing et al. 2019; Bisbing et al. 2022; Buma et al. 2018).

The 20 × 20 m site is a mixed fen dominated by yellow-cedars, which represents both major growth forms of the species (Figure 1). Total basal area is 39.54 m^2/ha, with arboreal yellow-cedar comprising ~75% of the total (29.15 m^2/ha). The tall, single-stemmed arboreal form is primarily dead due to snow loss and subsequent root freezing in the 1980s. A smaller component of mountain hemlock (*Tsuga mertensiana* Bong., 1.41 m^2/ha), western hemlock (*T. heterophylla* Raf., 6.74 m^2/ha), Sitka spruce (*Picea sitchensis* Bong., 0.65 m^2/ha), and unidentifiable snags (1.58 m^2/ha) are present (Bisbing et al. 2021). That same study also estimated mean canopy transmissivity via hemispherical photography for the plot, relevant for solar energy to the snowpack, at 64% (SD = 6%; see Bisbing et al. 2021 for details). The ground is entirely *Sphagnum* moss (consistent depth is > 10 cm, data not shown). A large amount of frutescent yellow-cedar is present and healthy, covering approximately 25% of the area and a consistent height of 0.4–0.6 m.

Four main experimental treatments were established, with five independent, randomly placed sensors in each: open ground (no coverage above, nor any within 3 m), intact thickets (under the frutescent form of yellow-cedar, no arboreal forms above), harvested thickets (the same condition as intact but with the yellow-cedar removed with clippers), and under dead tree-form yellow cedar (placed 2 m from the trunk on the north side, no shrub form). All sensors were placed in

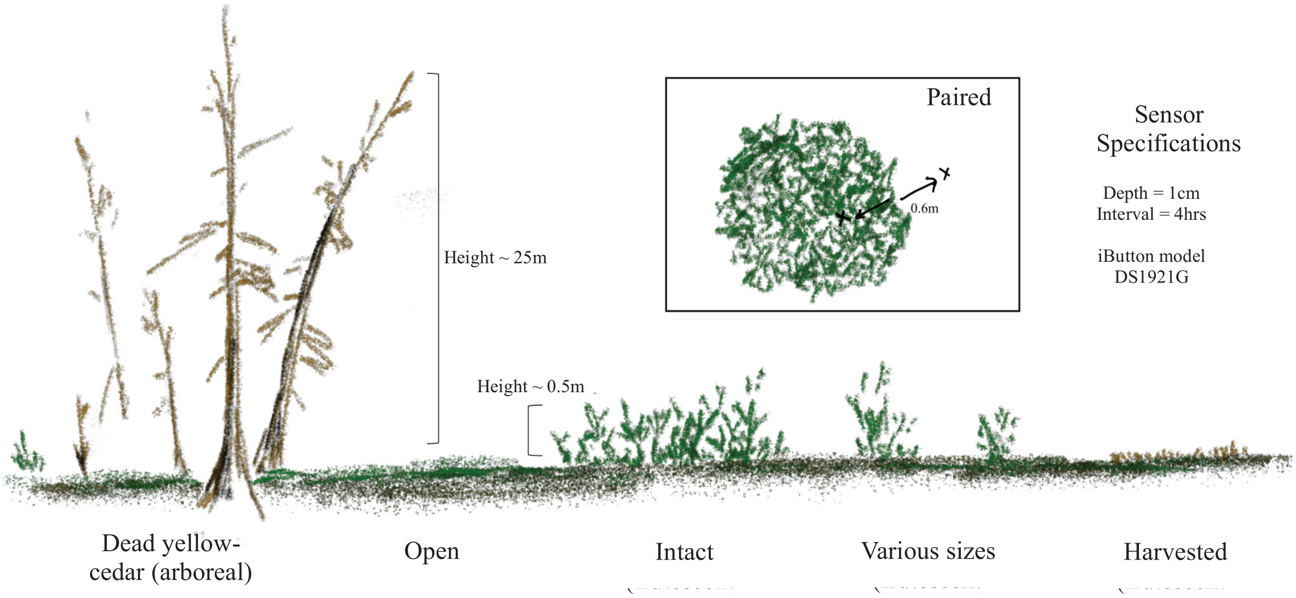

Figure 2. Treatments associated with the temperature loggers. The ground is a fen covered by *Sphagnum* mosses. Paired sensors are at 1 cm depth, located 60 cm horizontally (inside and outside) a patch.

separate, randomly selected patches to maintain independence while retaining the same potential snowfall inputs (e.g., snowfall inputs are not expected to vary at the scale of the plot; Figure 2). Three air temperature loggers were placed in a vented radiation shield hanging approximately 2 m above the ground.

Two sets of paired sensors were placed inside and outside (0.6 m horizontally from the edge) of an intact patch of frutescent yellow-cedar to pair a sheltered and nonsheltered measurement directly, similar to the above intact and open treatments (e.g., buried at 1 cm) but paired.

Ten more sensors were placed under random yellow-cedar shrubs of different volumes (length × width × height) to determine whether individuals provided temperature mediation on their own, ranging from 0.01 m^3 to 2.40 m^3.

Temperature loggers were iButtons (model DS1921G), set to record on a 4-hour increment, and installed in July 2021 and retrieved in May 2022. Temperature loggers were buried in the soil to a depth of ~1 cm to maintain surface temperature records while avoiding being taken by animals. The minimum temperature for each day was identified and used in subsequent analyses.

Analysis

The species is more sensitive to freezing soil in the spring (Schaberg et al. 2005), and so data was analyzed from March to mid-May, when sensors were collected. To determine differences between the treatments, if any, the number of days below zero was summed and averaged for each treatment. The Tukey's honestly significant difference (HSD) test was used to compare the number of days below freezing for each treatment, and a simple linear regression was used to examine any correlation between size and total freezing days (which is related to mortality likelihood; Schaberg et al. 2008). It is recognized that there is a small amount of autocorrelation within each treatment arising from "lag" associated with thermal inertia in soil temperatures. However, given that the data can be viewed directly (Table 1, Figure 3), this does not confuse direct interpretation of the results by the reader and is primarily intended as a summary value.

Table 1. Number of days below zero by treatment.

Treatment	Days below zero (SD)
Intact	1.4 (3.1)
Harvested	20.3 (7.3)
Dead	19.7 (4.5)
Open	12.0 (11.9)

Results

The intact patches of frutescent cedar were significantly warmer than the harvested locations and the area under dead arboreal cedar (Tukey's HSD, $P = 0.012$ and 0.025, respectively). Open sites were intermediate (Table 1), primarily due to very high variation between open sites (ranging from 1 day below zero to 29 days).

The majority of soil freezing days were associated with a late season cold snap (Figure 3) consistent with the yellow-cedar decline phenomenon, although one of limited duration and intensity. Air temperatures dropped to about −3°C for a short time in early March, and a longer period of time in mid-April. Harvested and dead treatments dropped the most, following the air temperature closely. The March snap appeared to be too short of a duration for substantial soil cooling, but the mid-April event did result in substantial soil freezing for multiple days. Two other slight air-temperature freezing events occurred in March but were very minimal and the soil did not cool substantially.

This sheltering effect is also clear when looking at the paired temperature sensors, one within a patch and one outside the same patch (0.6 m each). The outside temperature loggers are more closely aligned with air temperature and drop substantially during cold periods (Figure 4).

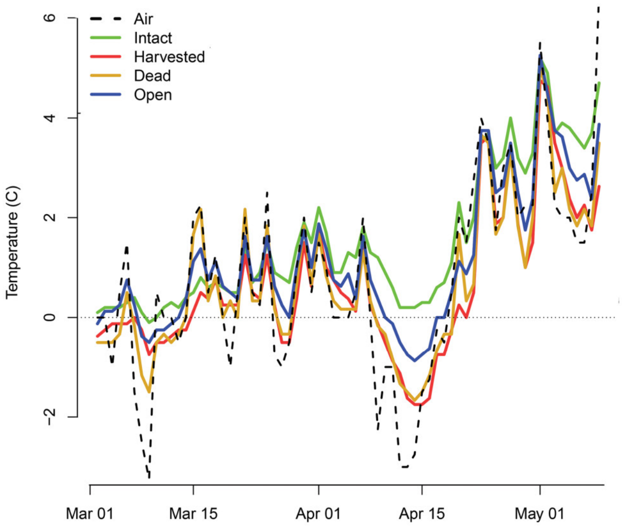

Figure 3. Mean minimum daily springtime temperatures in each treatment. A short cold snap in mid-April reduced air temperatures, which resulted in soil freezing in the harvested experimental treatment, open areas, and under dead arboreal yellow-cedar while the intact shrub-form yellow-cedar remained above freezing.

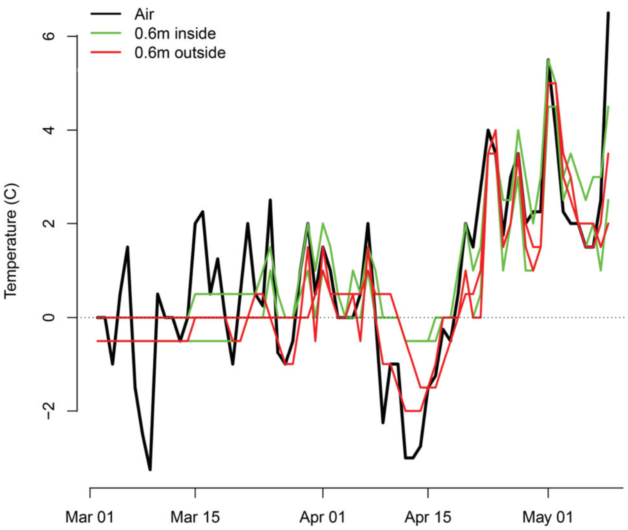

Figure 4. Paired sensors. Each line (except air) is an individual sensor. The interior sensors generally stay at or above freezing. The exterior sensors more directly follow air temperatures in mid-April cold snap.

Size of the patch was not significantly correlated with freezing days nor the lowest minimum temperature recorded.

Discussion

Snow loss and subsequent soil freezing can have dramatic effects on forests, including mass mortality. The results here support the hypothesis that the frutescent form may shield itself from cold spring temperatures, even without snow, providing an unexpected soil temperature refugia that may maintain the species on the landscape, albeit in a different form.

The intact treatments and the interior of the paired sensors remained generally at or above freezing throughout the spring, regardless of air temperatures (Figure 3). In contrast, soil in areas where the frutescent yellow-cedar had been removed was frozen for considerable amounts of time (Table 1), approximately 12 times more than the intact locations. This was mirrored in the areas where the arboreal yellow-cedar had died.

The long-term implications of this structural protection is unknown, perhaps favoring adaptation to new climates (Kuparinen et al. 2010). There is a high rate of clonality in bog environments; from 14% to 70% of stems can be clones produced via layering (Thompson et al. 2008). Yellow-cedar's vegetatively reproducing shrub form has been speculated as a way to survive harsh climates in the deep past (Hennon et al. 2016). Climate warming could drive a permanent situation where the species becomes less significant from a basal area perspective but is maintained as a shrub; alternatively, with continued warming, the cold snaps may cease and the arboreal form will recover ("transitional mortality," Buma 2018).

The temperatures observed were not enough to cause mortality in arboreal yellow-cedar, which generally requires several days around −5°C (Schaberg et al. 2008). The 2021–2022 winter was wet and with abnormally heavy snowfalls. Although there is no weather station at this elevation (250 m) in the region, it may be assumed that the snowfall at the site was high. Less snowy winters may produce a more exaggerated effect. Regardless, the temperature departures that were observed are the exact type of freezing event that causes mortality (were they to be slightly colder; Hennon et al. 2012). This study is therefore considered illustrative of typical mortality-causing spring freezing events, in type if not in magnitude.

It must be noted this is a single site and should be replicated across a larger range of frutescent densities, site contexts, and years. Although there is utility in exploring soil temperature variability using a small plot where snow inputs and soils are assumed to be basically equivalent, a broader range in space and time would allow an exploration of differences in snow densities, timing, canopy characteristics, and other factors that likely influence the efficacy of this sheltering mechanism.

Snow loss is becoming a global phenomenon (Thackeray et al. 2019). Because the mechanisms explored here are mechanical and structural, it is likely that these effects would be seen in other species as well.

Conclusions

Snow loss and subsequent soil freezing are causing mass mortality around the world. This study investigated one mechanism by which an alternative growth form can moderate direct impacts of climate change, namely soil temperatures, in an area that has transitioned from snow to rain. Results suggests that alternate growth forms may serve as an important if underappreciated way for species to persist as winters around the world shift from snow to rain.

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Conflict of Interest

None declared.

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