

Microsites and Climate Zones: Seedling Regeneration in the Alpine Treeline Ecotone Worldwide

Adelaide C. Johnson ^{1,*} and J. Alan Yeakley ²

¹ U.S.D.A., Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 11305 Glacier Hwy, Juneau, AK 99801, USA

² Department of Geography and Environmental Systems, University of Maryland Baltimore County, Baltimore, MD 21250, USA; yeakley@umbc.edu

* Correspondence: ajohnson03@fs.fed.us

Received: 9 September 2019; Accepted: 27 September 2019; Published: 3 October 2019

Abstract: Microsites, local features having the potential to alter the environment for seedling regeneration, may help to define likely trends in high-elevation forest regeneration pattern. Although multiple microsites may exist in any alpine treeline ecotone (ATE) on any continent, some microsites appear to enhance density of seedling regeneration better than others. Known seedling regeneration stresses in the ATE include low temperature, low substrate moisture, high radiation, drought, wind, and both high and low snowfall amount. Relationships among various microsite types, annual temperature, annual precipitation, and tree genera groups were assessed by synthesizing 52 studies from 26 countries spanning six continents. By categorization of four main microsite types (convex, concave, object, and wood) by mean annual precipitation and temperature, four major climatic zone associations were distinguished: cold & dry, cold & wet, warm & dry, warm & wet. Successful tree recruitment varied among microsite types and by climatic zones. In general, elevated convex sites and/or decayed wood facilitated earlier snow melt for seedlings located in cold & wet climates with abundant snowfall, depressions or concave sites enhanced summer moisture and protected seedlings from wind chill exposure for seedlings growing in cold & dry locations, and objects protected seedlings from excessive radiation and wind in warm & dry high locations. Our study results suggest that climate change will most benefit seedling regeneration in cold & wet locations and will most limit seedling regeneration in warm & dry locations given likely increases in fire and drought. Study results suggest that high-elevation mountain forests with water-limited growing seasons are likely to experience recruitment declines or, at best, no new recruitment advantage as climate warms. Climate envelope models, generally focusing on adult trees rather than seedling requirements, often assume that a warming climate will move tree species upward. Study results suggest that climate models may benefit from more physically-based considerations of microsites, climate, and current seedling regeneration limitations.

Keywords: climate change; climate zone; environmental stress; forest edge; precipitation; tree regeneration; tree seedling recruitment; upward advance

1. Introduction

Alpine treeline ecotone (ATE) locations are conspicuous high-elevation forest edges located on all continents except Antarctica [1]. The ATE extends from subalpine forest with trees of large stature moderating climatic stresses [2], up to treeline, the upper limit for tree growth (Figure 1). Between the forest line and treeline, the transitional ecotone may vary in width from tens to hundreds of meters [3]. ATE form can be abrupt, with an immediate transition from subalpine to alpine tundra or

diffuse, a gradual transition from subalpine to alpine meadows, and may contain krummholz (i.e., stunted struggling trees), and tree islands [4]. Growing season temperature is generally assumed to be the main limitation for seedling regeneration and forest growth at the treeline [5,6]. Other factors also determine the forest distribution locally, such as viability of seed supply, animal and insect herbivory, substrate moisture availability, solar radiation, wind, snow cover, snow glide, snow avalanching, rock fall, human influence, competition from neighbors, unfavorable soil properties, fire, and microsite availability [1,5,7–9].

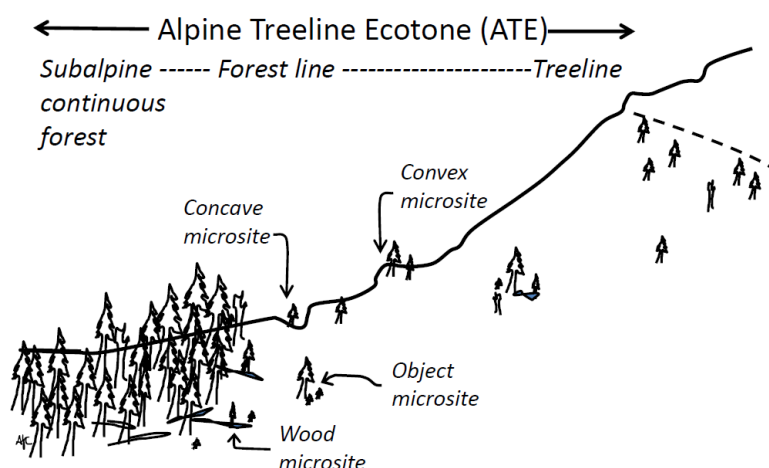


Figure 1. Timberline location and microsite type within the alpine treeline ecotone (ATE). Four microsite types summarized in this study are highlighted. Note ATE width, varying considerably worldwide, varies from abrupt to diffuse in structure. A diffuse ATE ecotone, typical of cool/wet climates is illustrated here.

Regeneration of seedlings represents a period of life where trees suffer the greatest mortality of all life stages [10]. Although climate projections often assume that the climate suitable for adult trees will be adequate for forest regeneration, seedling recruitment is often ignored, and given low seedling regeneration success at many locations, a demographic bottleneck for upward tree migration may exist [11]. Seedling regeneration and possible upward advance of forests associated with climate change is dependent on a few site-specific factors occurring within the broad ATE; these factors are highly heterogeneous spatially and temporally [12].

Microsites are local features/structures on the scale of centimeters to meters having the potential to alter the environment for seedling regeneration. Although multiple microsites may exist in any ATE on any continent, locally, some microsites appear to enhance density of seedling regeneration better than others. The type of microsite most associated with seedling regeneration may vary by local climate [5,7,8]. In general, enhancement of local moisture, increased growing season, and protection of seedlings from frost stress and wind are emphasized as key reasons for seedling survival on specific microsites. For example, in the U.S. Rocky Mountains and Ecuador, *Polylepis*, *Abies lasiocarpa* and *Picea engelmannii* were associated with facilitating effects of tree clumps [13–15]. In some areas, seedling regeneration occurs where objects such as rocks or canopy shade the ground, which reduce winter/spring sun radiation, night time heat loss, frost occurrence, photoinhibition, and subsequent tree death [16]. *Pinus albicaulis* survival in the Beartooth Plateau, Montana has been linked to caches of the Clark’s nutcracker on the leeward side of trees [17]. In the Caucasus Mountains of Georgia [18], Finnish Lapland [19], and the Cordoba Mountains of Argentina [20], *Betula litwinowii*, *Picea abies* and *Polylepis australis* seedlings, respectively, have been associated with small valleys and furrow microsites. In the Pacific Northwest (PNW), *Tsuga mertensiana* and *Abies lasiocarpa* have been associated with ridges and convexities [21,22]. Others have noted significant regeneration of *Abies lasiocarpa*, *Abies densa*, *Picea abies*, and *Rhododendron calophytum* on microsites formed by decayed wood in PNW alpine meadows, European Alps, and mountainous southwest China [23–25].

Although enhanced tree regeneration in alpine treeline ecotones (ATE) is associated with favorable microsites [26–28], there is no known global summary linking microsite type with local climate. Our study had three main objectives: (1) summarize main microsite types found worldwide, (2) determine any microsite and annual temperature and annual precipitation relationships that most often lead to successful seedling regeneration, and (3) evaluate evidence supporting the role of microsites in upward forest advance potential.

2. Materials and Methods

2.1. Global Dataset

The initial world-wide search of the scientific literature to discern key microsites in the ATE (objective 1) included search terms including: microsite, timberline, forest line, tree line, subalpine, alpine, mountain, seedlings, advance, precipitation, facilitation and regeneration. Alongside searches using general-purpose search engines, we used two main abstracting/indexing systems—ISI Web of Knowledge and Scopus—with a wide range of search strings. For each microsite type, site characteristics including location, elevation, dominant tree genus associated with regeneration, and type of regeneration were noted. For example, if an article highlighted significant regeneration in depressions (concavities), distance of seedling regeneration above the upper limit of the continuous forest was described as well as the type of forest edge (i.e., abrupt or dispersed), if possible.

When compiling the dataset, emphasis was placed on assembling a wide range of microsites worldwide. Hence, only one location/microsite/tree genus combination per region was selected. For example, only one of the multiple studies of object (or shade) microsites with *Picea* sp. among multiple studies on Niwot Ridge, Colorado, USA, was selected for the analysis. We drew a study from each combination at random. Sites with noted human disturbance and animal grazing were not selected for use in the dataset. Parameters compiled in the dataset included: microsite type, mean annual precipitation, mean annual temperature, elevation, and dominant tree genus (Supplemental Information). Other information, if listed, was compiled including: number of seedlings per microsite type, indications of positive tree regeneration by microsite. About 80% of the references had climate information. If precipitation or temperature was missing, either another local reference, DayMet (in western USA) [29], or WorldClim (global database) [30] was used.

Creation of the dataset involved some subjective interpretation. For example, if it was stated that most seedlings grew on convex microsites and regeneration appeared or was also implied to be influenced by overstory canopy, convex microsites were used in the analysis because this reference appeared most dominant. If a range of elevations were part of a study in the ATE, the highest microsite elevation was used in the analyses.

2.2. Data Analysis

Once the dataset was compiled, assessments of relationships among microsite type, annual temperature, annual precipitation, genus, and elevation were evaluated in three steps (objective 2) by: (1) testing for significant differences, (2) plotting 95% confidence intervals of annual temperature and precipitation for microsite types, and (3) visually splitting microsite populations to assess possible climate zone categorization. Upward forest advance potential (objective 3) was assessed by summarizing microsite—climate associations including: seedling density information; distance of regenerating seedlings from the forest; noted physiologic stresses; positive, negative, and negligible microsite attributes; and noted upward advance. Once summarized, implications of these associations were evaluated in the Discussion.

Significant statistical differences were evaluated among microsite type, tree genus, and mean annual precipitation and temperature by conducting separate one-way analysis of variance (ANOVA) tests among microsite type (four categories) with mean annual precipitation, mean annual temperature, and dominant genus groups (*Abies*, *Betula*, *Nothofagus*, *Picea*, *Pinus*, *Polylepis*, and *Tsuga*). Tests for meeting assumptions for normality and uniform variation were conducted and Post-hoc

multiple comparison tests (Tukey's) used when significant differences were detected. Statistical significance was assessed with $\alpha = 0.05$ and all statistical analyses were conducted with the R statistics package [31].

3. Results

Four microsite categories were summarized from the literature including: (1) convex (also elevations and mounds), (2) concave (also including furrows, depressions, and mires), (3) object (associated with vegetation, rocks or wood), and (4) wood substrates (including nurse logs) (Figure 1). The resulting dataset consisted of 52 ATE locations with climate data (Supplementary Information), spanning all continents ($n = 6$) except for Antarctica (Figure 2).

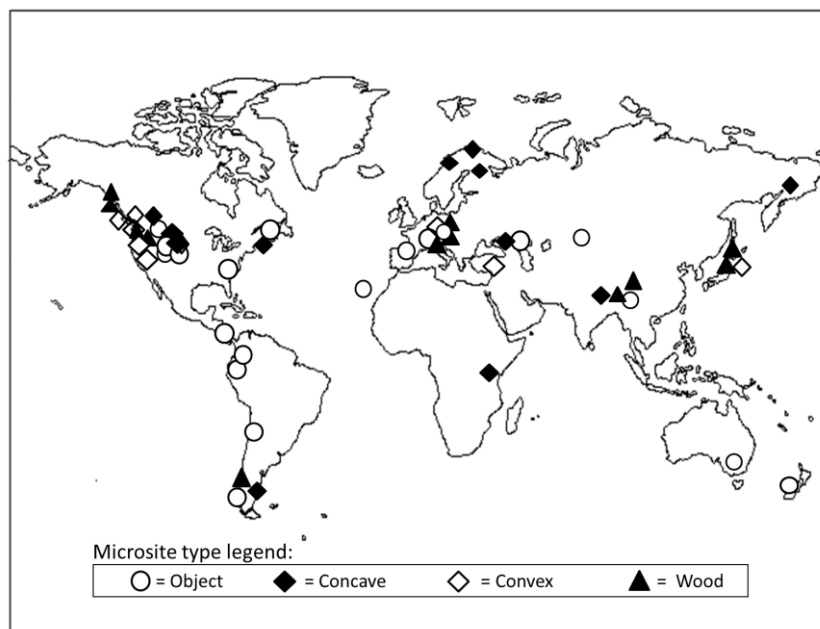


Figure 2. Dominant microsite types for seedling regeneration in the alpine treeline ecotone (ATE) around the world. Sites were selected by searching literature with initial search terms including: microsite, timberline, forest line, treeline, subalpine, alpine, mountain, seedlings, advance, precipitation, facilitation, and regeneration. Relevant literature was differentiated into four ATE microsite types (see Supplemental Information for associated references).

Mean annual temperature and precipitation at microsites ranged from $-4.0\text{ }^{\circ}\text{C}$ to $12\text{ }^{\circ}\text{C}$ and 14 cm to 439 cm, respectively (Table 1). Mean annual temperature was significantly different for microsites ($p = 0.01$) with object microsites having significantly greater temperatures than concave microsites ($p = 0.01$). Mean annual precipitation was different for microsite types ($p < 0.001$). Convex and wood microsites had more precipitation than concave microsites ($p < 0.01$ and $p < 0.001$, respectively), convex and wood microsites had greater precipitation than object microsites ($p = 0.03$ and $p < 0.01$, respectively). Mean annual precipitation for the *Abies* genus group was greater than the *Pinus* genus group ($p = 0.03$) and mean annual temperature for the *Pinus* genus group was greater than that of the *Picea* and *Betula* groups ($p < 0.01$, $p < 0.01$, respectively). Elevation was not associated with climate zone, microsite type, or genus group ($p > 0.07$).

Microsite type, positively associated with tree recruitment in certain climatic zones, was categorized by visually splitting 95% confidence intervals of microsite annual temperature and precipitation distributions (Figure 3). Climate categorization was as follows: warm & wet ($n = 8$), cold & wet ($n = 12$), warm & dry ($n = 14$), and cold & dry ($n = 18$). Climate zones separated wood/convex microsites, concave microsites, and object microsites. An annual temperature at approximately $4\text{ }^{\circ}\text{C}$ separated warm from cold climates and an annual precipitation of about 145 cm separated dry and

wet climates. The warm & wet climate zone had least noted microsite dominance ($n = 1$ for wood, $n = 4$ for object, and $n = 3$ for convex microsities) (Supplemental Information).

Table 1. Alpine treeline ecotone (ATE) microsite types enhancing seedling regeneration with mean annual temperature, precipitation, and elevation.

Microsite Type	Number Observations	Temperature Range, °C (mean/st.dev.)	Precipitation Range, cm (mean/st.dev.)	Elevation Range, m (mean/st.dev.)	Microsite Characteristics
Wood	12	0.1–5.0 (3.06/1.78)	86–439 (227/93.3)	873–3300 (1814/862)	Seedlings growing in decayed wood lying on ground.
Convex	10	−2.4–5.0 (2.77/1.65)	66–350 (208/99.8)	1195–3100 (1964/529)	Seedlings growing on elevations or mounds on ground surface.
Concave	11	−3.6–8 (1.37/4.1)	14–167 (87.4/34.5)	460–4200 (2185/901)	Seedlings growing in depressions, valleys, and furrows in the ground surface.
Object	19	−4.0–12 (6.1/4.98)	22–225 (123/55.6)	700–4100 (2465/896)	Association of seedlings with trees, plants, wood, or rocks.

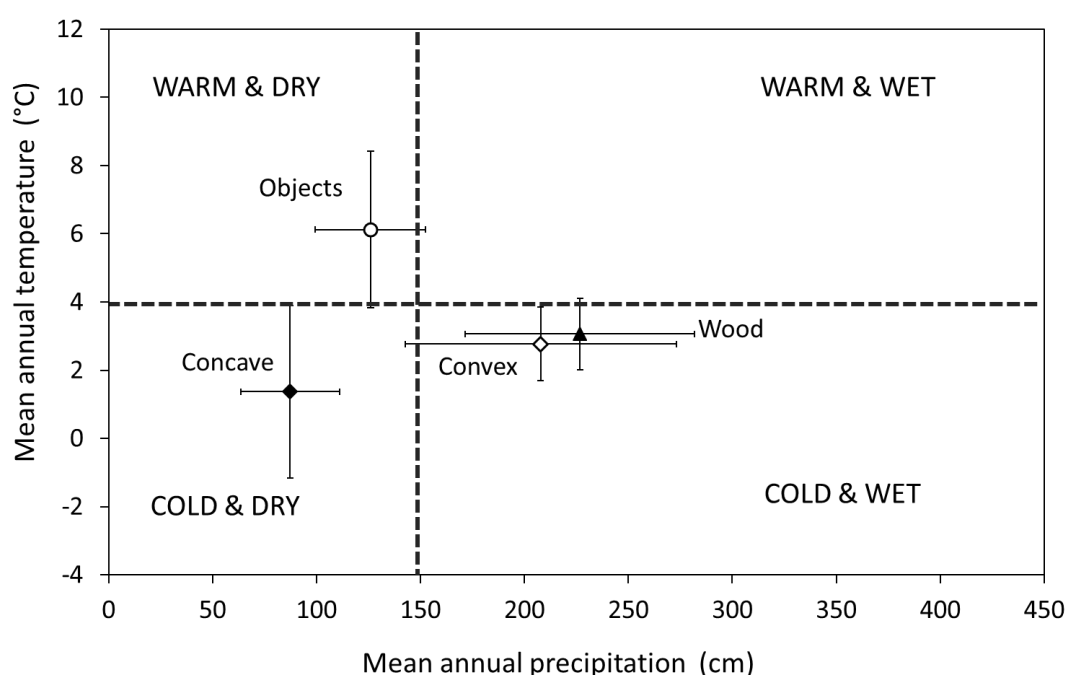


Figure 3. Alpine ecotone treeline microsite presence within four climate zones. Climate zones were differentiated (as indicated by dashed lines) by significant annual temperature differences between concavity and object microsities and significant annual precipitation differences for wood/convexity microsities and concavity/object microsities. Dashed lines indicate visual splits of precipitation and temperature based on microsite population groupings. Error bars indicate 95% confidence intervals.

For *Picea*, *Abies*, *Pinus*, and *Betula*, the most represented genus groups (4 out of 7), associations among continent, climate, and microsite were summarized. *Picea* ($n = 14$) was found mostly in cold & wet climates ($n = 7$) on wood microsities ($n = 4$) in the countries of Europe, North America, and Asia. *Abies* ($n = 10$), located in North America and Asia and in all climate zones and on all microsities, was located mostly in cold & wet elevations ($n = 5$). *Abies* was found on both convex microsities ($n = 3$) and wood microsite ($n = 2$) in North America and Asia. *Pinus* ($n = 7$), located in Europe, North America, and Asia, was found mostly in Europe ($n = 4$) at warm & dry locations in association with object microsities. *Betula* ($n = 5$), found in Asia, Europe, and North America, was located mostly in concave sites ($n = 4$) in cold & dry locations.

Microsite—climate associations along with noted seedling limiting factors and noted physiologic responses were summarized from the literature (Table 2). Warm & wet and warm & dry locations were generally associated with ample carbon assimilation [7,27,28], were limited by drought, had noted fire, were limited by humus substrates, and in some cases were limited by late snow melt. Seedlings in cold & wet and cold & dry locations had limits on carbon assimilation, infrequent seed crops, and suffered from stresses including photoinhibition, snow mold, and physical disturbance by snow.

Table 2. Summary of microsite type, associated climate zone, and noted site limitations.

Climate Category	Dominant Genus Noted, Typical Site Stress Ameliorated by Microsite	Noted upward Migration, Seedling Density, Seedling Survival Trends, Microsite Association	Noted Physiologic Response [2,27,28]
Warm & wet (wood/object/convex— no dominance)	Six species, no species dominance, moderate snow pack, moist	Seedling regeneration limited by humus late snow melt. Seedling regeneration greater on wood, object, and convex sites as compared to adjacent substrates.	Ample carbon assimilation.
Warm & dry (object)	Pinus Drought, fire	Greater seedling regeneration in proximity of trees or other objects; “low”, “downward”, and “unlikely”.	Ample carbon assimilation, photoinhibition, drought stress.
Cold & wet (convexity/wood)	Picea, Abies, Tsuga, high spring snowpack, low summer soil moisture	Seedling regeneration occurs beyond forests; “notable”, “possible”, “continuous recruitment”.	Limits on carbon assimilation, death by snow mold, death by snow damage, infrequent seed crops.
Cold & dry	Picea, Low growing season moisture and low temperature, high radiation.	Seedling regeneration occurs; “some in depressions”, “some where crypogams are present”.	Limits on carbon assimilation, poor, infrequent seed crops, photoinhibition, infrequent seed crops, drought stress.

4. Discussion

This global-scope microsite assessment serves to summarize essential seedling regeneration strategies that ameliorate site climate-related stresses in the alpine treeline ecotone (ATE). Although multiple microsites can be present in various climates, this study found tendencies of a specific microsite favoring regeneration to be in a particular climate zone. In general, elevated convex sites and/or decayed wood facilitate earlier snow melt for seedlings located in cold & wet climates with abundant snowfall, depressions or concave sites both enhance moisture and protect seedlings from wind chill exposure for seedlings growing in cold & dry locations, and objects protect seedlings from excessive radiation in warm & dry high locations. Microsite strategies enhancing successful regeneration: (1) help to categorize common climate-related physiologic stresses, (2) aid in assessments of possible upward movement of ATE, and (3) highlight possible climate adaptation strategies and restoration efforts.

Microsite—climate associations highlight typical physiologic stresses in the ATE (Table 2). For example, for sites in cold & wet locations, there is limited carbon uptake (carbon assimilation) of seedlings due to cold temperatures and time under snow [27], and these stresses appear to be ameliorated by convex sites [22]. Further, in cold & wet locations, snow mold infests seedlings particularly on concave sites, but seedlings are less prone to infestations on convex sites [32]. In particular, *Pinus cembra* can be attacked by *Phacidium infestans*, a fungus that infects needles and shoots of pines that are covered by snow for too long [33,34]. In warm & dry areas, objects such as trees and rocks serve to protect/facilitate seedling growth by protection from wind and high radiation pattern [1,35] and damage or death by photoinhibition. Photoinhibition, associated with periods of night frost followed by clear-sky days [36], is a notable cause of seedling death for seedlings in ATEs of Australia [36], Spain [37], and the North American Rocky Mountains [16]. Seedling association with objects that provide shade leads to less photoinhibition [16], substantial increases in

photosynthetic carbon gain throughout the summer growth period, enhanced root growth, amelioration of drought stress, and increased seedling survival [3]. In the colder and wetter locations such as the US Pacific Northwest, photoinhibition does not appear to be as common [23]. Mechanical damage of seedlings and trees is associated with wind abrasion of needle cuticles, apical bud damage, snow loading and frost heaving causing tissue and whole-tree mortality [7], stresses found to be ameliorated by both object microsites and concave microsites [7]. In the Dawodang Mountains of China and the Cascade Mountains of the US Pacific Northwest, greater stomatal conductance, for *Rhododendron calophytum* and *Abies lasiocarpa*, was attributed to the higher moisture provided by wood microsites than by adjacent soil substrates [23,25]. Future research could be enhanced by evaluation of both dominant and sub-dominant microsites having some effect on the pattern of seedling regeneration. Animal grazing, a dominant factor controlling treelines in many regions worldwide, was not in the scope of our analysis, but warrants further investigation in future studies.

Once physiologic stresses are alleviated, seedlings successfully regenerate. If trees survive to adulthood, there is potential for advance of the ATE. Although successful seedling generation does not mean that seedlings will grow to maturity, upward migration of forests to higher altitude must initially depend on new seedling establishment above the existing forest line into the treeline ecotone [3]. Given that global predictions of climate change forecast an increase in the frequency of extreme events such as heatwaves and frost, there could be a decrease in seedling establishment at alpine treelines [38,39]. Consistent with other research, our results suggest that high-elevation mountain forests with water-limited growing seasons are likely to experience recruitment declines or, at best, no new recruitment advantage as climate warms [11,40].

Although only a few (<10%) of the studies in this analysis explicitly describe potential for ATE advance, locations likely having least, moderate, and most upward advance is possible given the categorization of microsite type, climate zones, and current stresses (Table 2). Seedlings growing in concave and object microsites in locations that are most warm and dry likely have least potential for seedling regeneration as supported by the associated statements: “unlikely forest expansion” [20], “bottlenecks for tree recruitment” [41] and even “downward treeline migration” [42], attributes associated with fire and drought. Microsites in wetter warm & dry climate zones may indicate moderate, but steady regeneration with “little regeneration beyond 5m of trees” [10], where “greater survivorship of young seedlings was observed in microsites closer to tree islands or having overhead structures such as fallen stems” [43]. Where fire continues in such locations as the páramo of the Andes Mountains, treelines will not shift upwards; where fires are suppressed but no radiation-tolerant tree species are present, treelines will also not shift upwards; and even where fires are suppressed, and some radiation-tolerant tree species are present, treelines will shift upwards only slowly [44]. Cold & dry locations are expected to have moderate potential for upward advance, largely depending on presence of locations where species such as *Betula* grows in “wind-sheltered and steep concave slopes.” [45]. As shown by research in Nepal, little regeneration is occurring; what little regeneration does occur happens in association with periods of higher rainfall [46]. Cold & wet zones, particularly in ATE locations with > 150 cm/year precipitation likely have greatest potential for regeneration with climate warming given an increase in growing season with less snow. Seedling regeneration in cold & wet zones, where earlier snowmelt is facilitated, is described as “fairly continuous”, with a “disproportionate number of trees on mounds” [22,47], particularly in areas characterized by diffuse ATE form where regeneration is, “particularly responsive to overall temperature increases” [4].

Climate models, ecological theories, and suggestions for future research are illuminated by this worldwide microsite summary. With a general focus on growing requirements of adult trees rather than requirements of seedlings, climate envelope models frequently and inappropriately assume that a warming climate will move tree species upward [11]. This study, by focusing on favorable conditions for seedling survival as indicated by microsite type, provides a means to describe possible upward advance of forests. Microsite presence could be considered an ecological limiting factor helping to define specific growth limitations at any given time. Considering that microsites

ameliorate growth limitations in environments where seedling interactions are facultative and non-competitive in contrast to adult tree environments, more research describing both scale and optimal use of resources is warranted [48,49]. In addition, further research is needed to decipher the physiologic stresses occurring in the transition between seedlings to adult trees. As trees grow taller than ~3m, microsite effects may become negligible since taller crowns decouple trees from the near-ground surface climate and are more deeply immersed within the prevailing atmosphere [40,50], when the local climate (mesoclimate) associated with topography begins to determine tree growth [51]. At some transitional stage, trees may be influenced by landforms larger than microsites, but smaller than mountain slopes. Additional information is needed on seedling requirements during both the summer and winter. In some cases, seedling establishment is more sensitive to winter conditions, notably to the length of snow cover than summer temperatures, so regional-scale factors such as winter climate and biotic interactions should be included in modelling exercises to improve future treeline location forecasts [52,53]. Further, while uniformity of climatic data (i.e. use of the same observation periods), comparison of seedling density on different microsites, and examination of time and scale of microsite/climate associations was not in the scope of this study, these methods would help to make comparisons among microsites. Given climate warming and greater evaporative demand, associated microsite preferences may be altered. For example, current seedling regeneration on some wood microsites may transition to greater seedling regeneration on object microsites [23,54]. Study results highlight some practical applications of microsite use in climate adaptation strategies and restoration actions. Given a large variation of micro-climatic conditions in alpine landscapes, areas of refugia will likely be present, so rather than forcing all species upslope to track climatic warming [55], these refugia may offer climate adaptation options. For example, one measure for improving *Pinus albicaulis* seedling regeneration success includes planting seedlings near standing trees [56]. Further, wood microsites, providing moister and warmer substrates, can be used in restoration practices. For example, in boreal and alpine areas where histories of fire suppression, forest harvest, and mechanical degradation of alpine meadows have occurred, newer policies encouraging controlled burns and natural succession processes, restoration practices have been benefitted by utilizing downed wood and wood fabric [54,57,58]. At these locations, wood microsites have effectively enhanced the rate of plant colonization.

5. Conclusions

By summarizing annual temperature and precipitation for key microsite types (object, concave, convex, and decayed wood) in a global context in the alpine treeline ecotone (ATE), four climate zones were illuminated: cold & dry, warm & dry, cold & wet, and warm & wet. Although microsite type and genus groups can be present in various climates, our findings suggest general tendencies of a specific microsite favoring seedling regeneration to be found within specific climates zones, and aid in better understanding of the potential for upper forest advance of the ATE. Warm & wet and warm & dry locations with warmth enabling seedling carbon assimilation were limited by drought, fire, humus substrates, and late snow melt; these are sites where regeneration was enhanced by object microsites. Seedlings in cold & wet (dominated by wood and convex microsites) and cold & dry (dominated by concave microsites) locations had limits on carbon assimilation, infrequent seed crops, and suffered from stresses including photoinhibition, snow mold, and physical disturbance by snow. Although the level that a microsite can ameliorate local stresses will vary in a changing climate, cold & wet climate zones with *Abies*, *Tsuga*, and *Picea* seedlings in ATE locations with > 150 cm/year precipitation likely have greatest potential for regeneration with climate warming given an increase in growing season with less snow. Study results highlight some practical applications of microsite use in climate adaptation strategies and restoration actions including use of objects providing shade particularly for *Pinus* seedling regeneration and use of rotten wood for *Picea* and *Abies* seedling regeneration. Considering that seedling mortality is much greater than for that of adult trees, further investigation of multiple driving mechanisms for advance and retreat is needed for better prediction of Earth's future forests in alpine areas.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1.

Author Contributions: Conceptualization, A.C.J. and J.A.Y.; Methodology, A.C.J.; Software, A.C.J.; Validation, A.C.J., and J.A.Y.; Formal Analysis, A.C.J.; Investigation, A.C.J.; Resources, A.C.J.; Data Curation, A.C.J.; Writing—Original Draft Preparation, A.C.J.; Writing—Review & Editing, J.A.Y.; Visualization, A.C.J.; Supervision, J.A.Y.; Project Administration, A.C.J.; Funding Acquisition, A.C.J.

Acknowledgments: This manuscript was benefitted from review and discussions with Ryan Bellmore, Alina Canter, Sarah Eppley, Andrew Fountain, Joseph Maser, Yangdong Pan, and by comments received by two anonymous reviewers.

Conflicts of Interest: The authors declare no conflict of interest

References

- Holtmeier, F. Mountain timberlines: Ecology, patchiness, dynamics. In *Advances in Global Change Research*; Springer Science & Business Media: Berlin, Germany, 2009; Volume 36, pp. 5–10.
- Tranquillini, W. *Physiological Ecology of the Alpine Timberline: Tree Existence at High Altitudes with Special Reference to the European Alps*; Springer Science & Business Media: Berlin, Germany, 2012; Volume 31.
- Smith, W.K.; Germino, M.J.; Hancock, T.E.; Johnson, D.M. Another perspective on altitudinal limits of alpine timberlines. *Tree Physiol.* **2003**, *23*, 1101–1112.
- Harsch, M.A.; Bader, M.Y. Treeline form—A potential key to understanding treeline dynamics. *Global Ecol. Biogeogr.* **2011**, *20*, 582–596.
- Holtmeier, F.; Broll, G. The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, USA. *Arctic Alpine Res.* **1992**, *24*, 216–228.
- Körner, C.; Paulsen, J. A world-wide study of high altitude treeline temperatures. *J. Biogeogr.* **2004**, *31*, 713–732.
- Malanson, G.P.; Butler, D.R.; Fagre, D.B.; Walsh, S.J.; Tomback, D.F.; Daniels, L.D.; Bunn, A.G. Alpine treeline of western North America: Linking organism-to-landscape dynamics. *Phys. Geogr.* **2007**, *28*, 378–396.
- Johnson, A.; Yeakley, A. Wood microsites at timberline-alpine meadow borders: Implications for conifer seedling regeneration and alpine meadow conifer invasion. *Northwest Sci.* **2013**, *87*, 140–160.
- Andrus, R.A.; Harvey, B.J.; Rodman, K.C.; Hart, S.J.; Veblen, T.T. Moisture availability limits subalpine tree establishment. *Ecology* **2018**, *99*, 567–575.
- Germino, M.J.; Smith, M.K.; Resor, C.A. Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecol.* **2002**, *162*, 157–168.
- Kueppers, L.M.; Conlisk, E.; Castanha, C.; Moyes, A.B.; Germino, M.J.; De Valpine, P.; Torn, M.S.; Mitton, J.B. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. *Glob. Chang. Biol.* **2017**, *23*, 2383–2395.
- Walther, G.R.; Post, E.; Convey, P.; Menzel, A.; Parmesan, C.; Beebee, T.J.; Fromentin, J.M.; Hoegh-Guldberg, O.; Bairlein, F. Ecological responses to recent climate change. *Nature* **2002**, *416*, 389–395.
- Cierjacks, A.; Iglesias, J.E.; Wesche, K.; Hensen, I. Impact of sowing, canopy cover and litter on seedling dynamics of two *Polylepis* species at upper tree lines in central Ecuador. *J. Trop. Ecol.* **2007**, *23*, 309.
- Daly, C.; Shankman, D. Seedling establishment by conifers above tree limit on Niwot Ridge, Front Range, Colorado, USA. *Arctic Alpine Res.* **1985**, *17*, 389–400.
- Maher, E.L.; Germino, M. J.; Hasselquist, N.J. Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine tree-line ecotone. *Can. J. Forest Res.* **2005**, *35*, 567–574.
- Germino, M.J.; Smith, M.K. Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant Cell Environ.* **1999**, *22*, 407–415.
- Mellmann-Brown, S. Regeneration of whitebark pine in the timberline ecotone of the Beartooth Plateau, USA: Spatial distribution and responsible agents. In *Mountain Ecosystems: Studies in Treeline Ecology*; Broll, G., Keplin, B., Eds.; Springer: New York, NY, USA, 2005.

18. Hughes, N.M.; Johnson, D.M.; Akhalkatsi, M.; Abdaladze, O. Characterizing *Betula litwinowii* seedling microsites at the alpine-treeline ecotone, central Greater Caucasus Mountains, Georgia. *Arct. Antarct. Alpine Res.* **2009**, *41*, 112–118.
19. Autio, J.; Colpaert, A. The impact of elevation, topography and snow load damage of trees on the position of the actual timberline on the fells in central Finnish Lapland. *Fennia* **2005**, *183*, 15–36.
20. Enrico, L.; Funes, G.; Cabido, M. Regeneration of *Polylepis australis* Bitt. in the mountains of central Argentina. *For. Ecol. Manag.* **2004**, *190*, 301–309.
21. Lowery, R.F. Ecology of subalpine zone tree clumps in the north Cascade Mountains of Washington. Ph.D. Thesis, University of Washington, Seattle, WA, USA, 1972.
22. Rochefort, R.M.; Peterson, D.L. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, USA. *Arctic Alpine Res.* **1996**, *28*, 52–59.
23. Johnson, A.C.; Yeakley, J.A. Seedling regeneration in the alpine treeline ecotone: Comparison of wood microsites and adjacent soil substrates. *J. Mt. Res. Development* **2016**, *36*, 443–452.
24. Motta, R.; Berretti, R.; Lingua, E.; Piussi, P. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. *Forest Ecol. Manag.* **2006**, *235*, 155–163.
25. Ran, F.; Wu, C.; Peng, G.; Korpelainen, H.; Li, C. Physiological differences in *Rhododendron calophytum* seedlings regenerated in mineral soil or on fallen dead wood of different decaying stages. *Plant Soil* **2010**, *337*, 205–215.
26. Rochefort, R.M.; Little, R.T.; Woodward, A.; Peterson, D.L. Changes in subalpine tree distribution in western North America: A review of climatic and other causal factors. *Holocene* **2004**, *4*, 89–100.
27. Franklin, J.F.; Moir, W.H.; Douglas, G.W.; Wiberg, C., Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arctic and Alpine Research*, **1971**, *3*, .215–224.
28. Moir, W.H.; Rochelle, S.G.; Schoettle, A.W. Microscale patterns of tree establishment near upper treeline, Snowy Range, Wyoming, USA. *Arct. Antarct. Alpine Res.* **1999**, *31*, 379–388.
29. DAYMET. Available online: www.daymet.org. (accessed on 2 February 2012).
30. WorldClim. Available online: www.worldclim.org (accessed 1 July 2018).
31. R Core Development Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2005; Available online: <http://www.R-project.org> (accessed on 10 August 2018).
32. Hiller, B.; Mütterthies, A. Humus forms and reforestation of an abandoned pasture at the alpine timberline (Upper Engadine, Central Alps Switzerland). In *Mountain Ecosystems: Studies in Treeline Ecology*; Springer: Berlin/Heidelberg, Germany, 2005; Volume 2, pp. 203–218.
33. Roll-Hansen, F. *Phacidium infestans*—A literature review. *Eur. J. For. Pathol.* **1980**, *19*, 237–250.
34. Barbeito, I.; Brückner, R.L.; Rixen, C.; Bebi, P. Snow fungi—Induced mortality of *Pinus cembra* at the alpine treeline: Evidence from plantations. *Arct. Antarct. Alpine Res.* **2013**, *45*, 455–470.
35. Hunziker, U.; Brang, P. Microsite patterns of conifer seedling establishment and growth in a mixed stand in the southern Alps. *For. Ecol. Manag.* **2005**, *210*, 67–79.
36. Ball, M.C.; Hodges, V.S.; Laughlin, G.P. Cold induced photoinhibition limits regeneration of snow gum at tree-line. *Funct. Ecol.* **1991**, *5*, 665–668.
37. Batllori, E.; Camarero, J.J.; Ninot, J.M.; Gutiérrez, E. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. *Glob. Ecol. Biogeogr.* **2009**, *18*, 460–472.
38. Inouye, D.W. The ecological and evolutionary significance of frost in the context of climate change. *Ecol. Lett.* **2000**, *3*, 457–463.
39. IPCC. Climate Change 2013: The physical science basis. In *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*; Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauks, A., Xia, Y., Bex, V., Midgley, P.M., Eds.; Cambridge University Press: Cambridge, UK, 2013; p. 1535.
40. Wieser, G.; Holtmeier, F.-K.; Smith, W.K. Treelines in a changing global environment. In *Trees in a Changing Environment*; Springer: Dordrecht, The Netherlands, 2014; pp. 221–263.
41. Cuevas, J. G. Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. *Journal of Ecology*, **2000**, *88*, 840–855.-

42. Hemp, A. Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. *Glob. Change Biol.* **2005**, *11*, 1013–1023, doi:10.1111/j.1365-2486.2005.00968.x.
43. Wearne, L.J.; Morgan, J.W. Recent forest encroachment into subalpine grasslands near Mount Hotham, Victoria, Australia. *Arct. Antarct. Alpine Res.* **2001**, *33*, 369–377.
44. Bader, M.Y.; Ruijten, J.J. A topography-based model of forest cover at the alpine tree line in the tropical Andes. *J. Biogeogr.* **2008**, *35*, 711–723.
45. Kullman, L.; Öberg, L. Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: A landscape ecological perspective. *J. Ecol.* **2009**, *97*, 415–429.
46. Liang, E.; Dawadi, B.; Pederson, N.; Eckstein, D. Is the growth of birch at the upper timberline in the Himalayas limited by moisture or by temperature? *Ecology* **2014**, *95*, 2453–2465.
47. Brett, R. B., and K. Klinka. A transition from gap to tree-island regeneration patterns in the subalpine forest of south-coastal British Columbia. *Canadian Journal of Forest Research* **1998**, *28*, 1825–1831.
48. Danger, M.; Daufresne, T.; Lucas, F.; Pissard, S.; Lacroix, G. Does Liebig's law of the minimum scale up from species to communities? *Oikos* **2008**, *117*, 1741–1751.
49. Choler, P.; Michalet, R.; Callaway, R.M. Facilitation and competition on gradients in alpine plant communities. *Ecology* **2001**, *82*, 3295–3308.
50. Yu, D.; Wang, Q.; Wang, X.; Dai, L.; Li, M. Microsite Effects on Physiological Performance of *Betula ermanii* at and Beyond an Alpine Treeline Site on Changbai Mountain in Northeast China. *Forests* **2019**, *10*, 400, doi:10.3390/f10050400.
51. Li, X.; Liang, E.; Gricar, J.; Rossi, S.; Cufar, K.; Ellison, A. Critical minimum temperature limits xylogenesis and maintains treelines on the Tibetan Plateau. Available online: <https://www.biorxiv.org/content/early/2016/12/13/093781.full.pdf> (accessed on 7 April 2019).
52. Hijmans, R.J.; Graham, C.H. The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Chang. Biol.* **2006**, *12*, 2272–2281.
53. Renard, S.M.; McIntire, E.J.; Fajardo, A. Winter conditions—not summer temperature—influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec. *J. Veg. Sci.* **2016**, *27*, 29–39.
54. Marzano, R.; Garbarino, M.; Marcolin, E.; Pividori, M.; Lingua, E. Deadwood anisotropic facilitation on seedling establishment after a stand-replacing wildfire in Aosta Valley (NW Italy). *Ecol. Eng.* **2013**, *51*, 117–122. ISSN 0925-8574.
55. Scherrer, D.; Körner, C. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *J. Biogeogr.* **2011**, *38*, 406–416.
56. Keane, R.E.; Tomback, D.F.; Aubry, C.A.; Bower, A.D.; Campbell, E.M.; Cripps, C.L.; Jenkins, M.B.; Mahalovich, M.F.; Manning, M.; McKinney, S.T.; et al. *A Range-Wide Restoration Strategy for Whitebark Pine (Pinus albicaulis)*; General Technical Report RMRS-GTR-279; US Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2012; 108p., 279.
57. Fattorini, M. Establishment of transplants on machine-graded ski runs above timberline in the Swiss Alps. *Restor. Ecol.* **2001**, *9*, 119–126.
58. Vanha-Majamaa, I.; Lilja, S.; Ryöma, R.; Kotiaho, J.S.; Laaka-Lindberg, S. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: The EVO experiment. *For. Ecol. Manag.* **2007**, *250*, 77–88.



© 2019 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).