

Short Communication A

WINTER DROUGHT IMPAIRS PINE REGENERATION AT THE PYRENEAN TREELINE

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COLD STRESS CONSTRAINS TREE ESTABLISHMENT IN ALTITUDINAL TREELINES

In cold environments, winter conditions may cause plants to suffer water stress, as more water is lost from leaves to atmosphere than is gained from soil to roots. In spite of low water demand due to low air temperatures, plants cannot compensate even small losses from frozen soil (Sakai & Larcher 1987: 238; Mayr 2007). This affects evergreens more than it affects deciduous trees and shrubs, since evergreens maintain much larger transpiration surfaces through winter. It is therefore not surprising that leaves from evergreen plants in cold environments invest heavily in drought defence even though they are not water stressed during the growing season. Common defensive foliar structures are stony hypodermis (e.g. in *Pinus* and *Juniperus* species) or well-developed cuticular wax layers (widespread over taxa).

Defence adaptations are mostly shown in trees and shrubs; herbs and sub-shrubs remain protected against winter water losses, at least where the snow pack is widespread and long-lasting. However, winter winds carrying small snow crystals are known to cause cuticular wax abrasion on protruding plants (Hadley & Smith 1989). Such insulation worsening results in noticeable water losses, and then in xylem cavitation leading to the death of leaves, twigs and entire branches. These effects have been variously studied near the upper forest limits in temperate and boreal zones, and are termed winter desiccation or frost drought (Tranquillini 1980, Siegwolf & Larcher 1987, Mayr et al. 2003, Neuner 2007). Winter desiccation is especially virulent just above the snow blanket, and decreases exponentially from there upwards (Scott et al. 1993, Smith et al. 2003). Its consequences are easily seen after severe winters in the form of damage in saplings and lower tree branches, while upper branches

remain apparently undisturbed (Figure 1). This is one of the causes of the development of *krummholz*, or low, multi-stemmed growing forms of subalpine trees, which are so common in alpine timberlines (Holtmeier 2003).



Figure 1. *Pinus uncinata* krummholz partially damaged due to winter drought.

In addition, freeze-thawing cycles promote embolism in the xylem of conifers, via the formation of gas microbubbles in the tracheids during sap thawing. This results in more severe damage the higher the number of cycles and the longer the winter periods with mild temperatures are (Sparks & Black 2000, Mayr et al. 2006). Climate records from high mountain sites show an ongoing increase of spring (and fall) periods of relatively high daytime temperatures with the soil remaining frozen (Diaz & Bradley 1997). This rising trend would explain that in recent years, severe winter drought has affected *Pinus uncinata* individuals at the Pyrenean timberline. This has been assumed to be the main cause of the generalized mortality of coniferous populations near the forest limit, apparently a long-term recurrent phenomenon due to climatic variability (Kullman 1989).

At the Pyrenean treeline, small *Pinus uncinata* (krummholz, saplings, seedlings) and the shrubs *Rhododendron ferrugineum* and *Juniperus communis* ssp. *alpina* show a complex pattern of disturbance drawn by dead twigs or branches due to winter desiccation. The distribution and frequency of such damages depends on the aerial architecture of the plants, and on the height, space distribution and timing of the protecting snow blanket (Holtmeier & Broll 2005). Moreover, surface roughness, the complex structure of the forest-heath-pasture ecotone and weather events (including storms, extreme winds or cold blizzards, etc.) provide

little chance for *Pinus* and other evergreens to regenerate (Germino et al. 2002, Smith et al. 2003). This partly explains why timberline has remained relatively static over the past century, despite decades of pasture abandonment and rising temperatures (Camarero & Gutiérrez 2004).

The heterogeneous space distribution of small pines within the treeline ecotone –mainly clumped– also supports passive facilitation, by means of (mutual) sheltering and fixation of snow through windy weather (Noble 1980, Scott et al. 1993, Holtmeier 2003, Smith et al. 2003). We put forward the hypothesis that the survival of *Pinus uncinata* seedlings and small saplings above the forest limit strongly depends of that sheltering, i.e. the closer they are to taller pines or shrubs the greater their chances of survival.

SEEDLING EXPERIMENTS

We performed two field experiments at the treeline ecotone of the Central Pyrenees to test the influence of the precise location of small pines on their survival and fitness, with respect to winter harshness. The experimental plot was located at Serrat de Capifonts (Pallars Sobirà, NE Spain, UTM: 367545 E, 4712092 N) in an area that slopes steadily upwards to the South, and is a good example of a semi-natural treeline ecotone. From 2,350 to 2,450 m a.s.l., the plot encompassed subalpine *Pinus uncinata* forest ranging to alpine pastures, through irregular alternation of contrasting vegetation spots (forest, ericaceous dwarf heath, pasture). This ecotone also offered contrasting environmental conditions on a small scale: soil quality (bedrock more or less superficial, even exposed), light conditions (related to varying vegetation structure and density), snow redistribution and persistence, and temperatures.

Soil temperatures vary daily and yearly much less than air temperatures at the canopy height do, particularly during winter. The records of 2006 (Figure 2) show that air temperatures above the snow cover oscillated widely all round the year, with 132 days of freeze-thawing processes. These cycles occurred during autumn and from midwinter to late spring, with frequent extremes lower than -6 °C and higher than 10 °C. In contrast, the soil (at a depth of 10 cm) remained rather static; near zero degrees for 6 months. At a few centimetres above ground level under the canopy of *Rhododendron ferrugineum*, thermal evolution was similar to that of the soil for 4-5 months, but it reflected the pattern of atmospheric temperatures in autumn and late spring. This depended on the duration of the snow cover. Under this low shrub, known to be very sensitive to winter freezing and thus a good indicator of regular and long-lasting snow cover, there were 49 freeze-thawing cycles during 2006. These were more frequent (65 cycles) at the spots covered by *Loiseleuria procumbens*, a dwarf shrub typical of areas with irregular snow cover, thus more resistant to frost damage (Körner 2003).

Regeneration of *Pinus uncinata* preferably takes place within the treeline ecotone. Seedlings, saplings and krummholz are abundant there, whereas they become very rare both lower down in the forest, and higher up in the pastures (Ninot et al., in press).

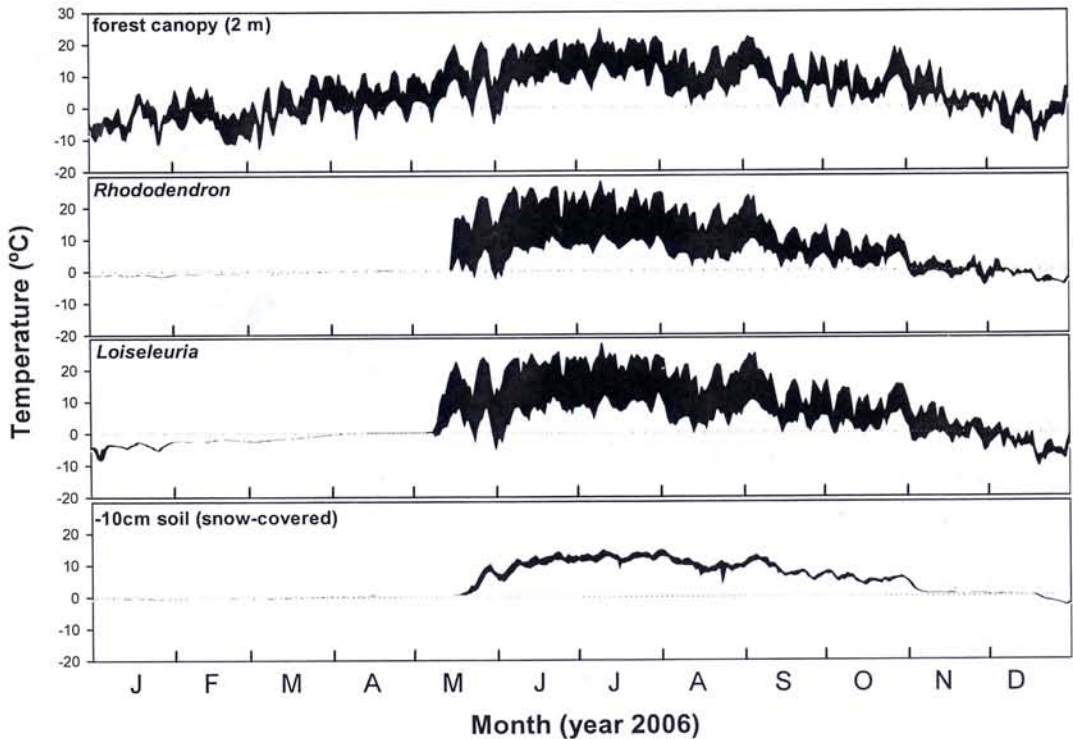


Figure 2. Daily thermal amplitude (black area) during 2006 at various positions in the plot studied (elevated 2 m above the soil, on the soil in a *Rhododendron* place, on the soil in a *Loiseleuria* place, 10 cm deep under *Rhododendron*), to illustrate the extent of freezing-thawing cycles in winter.

The first experiment consisted of transplanting *Pinus uncinata* seedlings grown for 3-4 years in a tree nursery, and mostly 20-30 cm high, at various positions with respect to krummholz specimens. Around each such 'nurse' krummholz, we located one seedling at each of the 12 points resulting from the combination of three distances (25, 50 and 100 cm) and four cardinal directions: upwards (= leeward), downwards (= windward), right and left from the krummholz crown. We set 30 of these groups ($n = 360$ seedlings) in autumn 2004 and 30 more in autumn 2005, which are treated as distinct cohorts thereafter.

The seedlings transplanted in 2004 suffered strong winter effects, which resulted in more than 60% of them dying. In February 2005, strong north winds swept most of the snow cover from the plot, and left the small pines exposed to very low temperatures and to the desiccating atmosphere, enhanced by the abrasive effects of wind-blown ice particles. In contrast, only about 30% of the second cohort died after their first year. The snow thickness and duration during the mild 2005-2006 winter was similar to the long-term average. Irrespective of winter severity, seedlings survival was significantly ($p < 0.05$) higher near to the nurse krummholz (25 cm) than at the other distances (50 or 100 cm; Figure 3A). However, the direction of plantation caused even greater differences among the groups (Figure 3B). The seedlings planted leewards survived significantly more ($p < 0.001$) than those situated in the other directions. This was clearly related to the effect of the dominant northerly winter winds in the study plot. For instance, during the 2004-2005 winter, strong winds swept away almost all of the snow cover around the krummholz mats, except for irregular drifts to the south of each krummholz (leeward). This explains that in the first cohort, 56.7% of the transplanted

seedlings survived for leeward positions, compared to 18.1% for the other positions. However, differences in first year survival rates in the second cohort due to plantation distance and direction were not as pronounced after the milder winter of 2006; 83.3% of the planted individuals survived to leeward and 66.3% survived in the other positions.

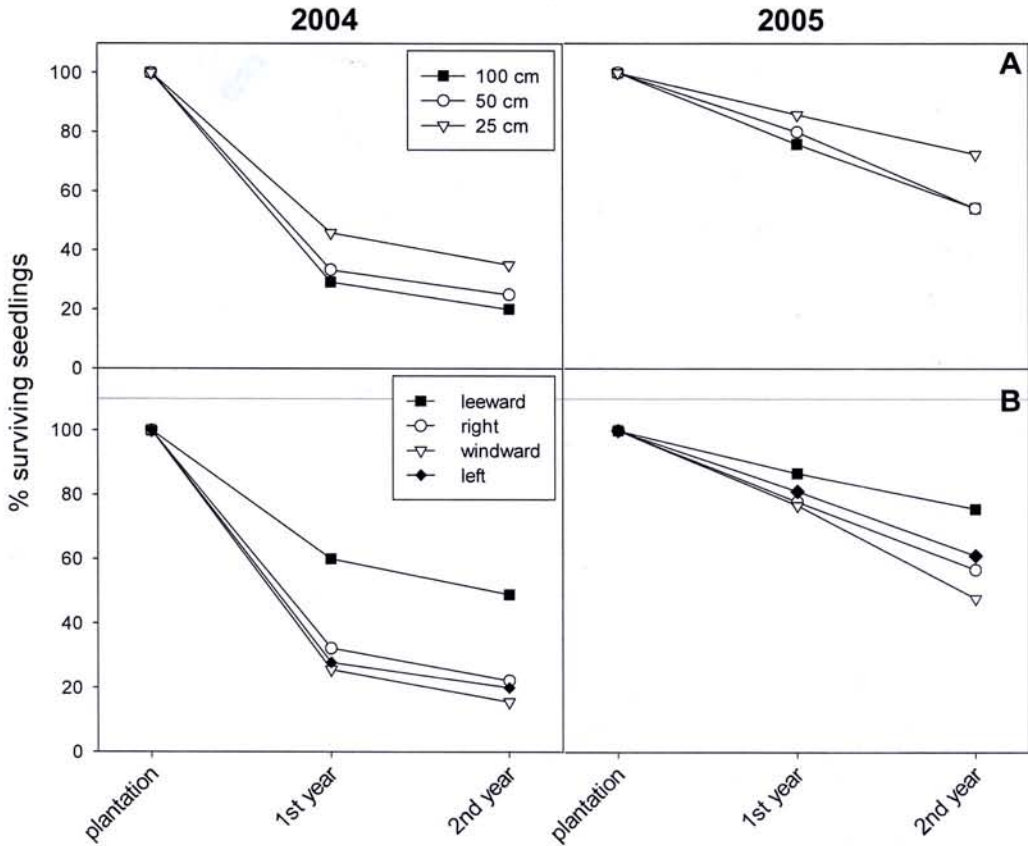


Figure 3. Survival percentage of the transplanted *Pinus uncinata* seedlings during the two first years according to positions around the nurse krummholz, in two cohorts ($n = 360$ each): autumn 2004 (left) and autumn 2005 (right). Seedlings position is grouped according to distance (A) and to orientation (B). The surveys of seedlings survival were carried out at the end of each growing season.

This first experiment also included two groups of 50 seedlings planted without the protection of any krummholz or shrub; one in the ecotone and the other above the treeline. Mortality was clearly higher in both groups ($> 90\%$) than for any of the other seedling locations.

In the second experiment, we transplanted *P. uncinata* seedlings in autumn 2006. These were smaller seedlings, mostly 10–18 cm high, and we set them close to *Rhododendron ferrugineum* shrubs. For each shrub we planted six seedlings just at the edge of the shrub crown (sheltered), and six seedlings 60 cm from the crown (unsheltered). We set 16 of these groups in the treeline ecotone ($n = 90$ seedlings), and 16 within the neighbouring forest (below the timberline). Most of the seedlings survived after the first winter (2007), with just a few deaths in the harsher conditions (unsheltered and in the ecotone). Also, winter damage

due to desiccation only occurred in the treeline ecotone. The percentage of dead leaves after winter reflected a definite nursing effect of *Rhododendron* on the transplanted seedlings in this ecotone. In unsheltered positions, 55% of the seedlings showed some damage, whereas 96% of the seedlings were undamaged at the sheltered positions (Figure 4).

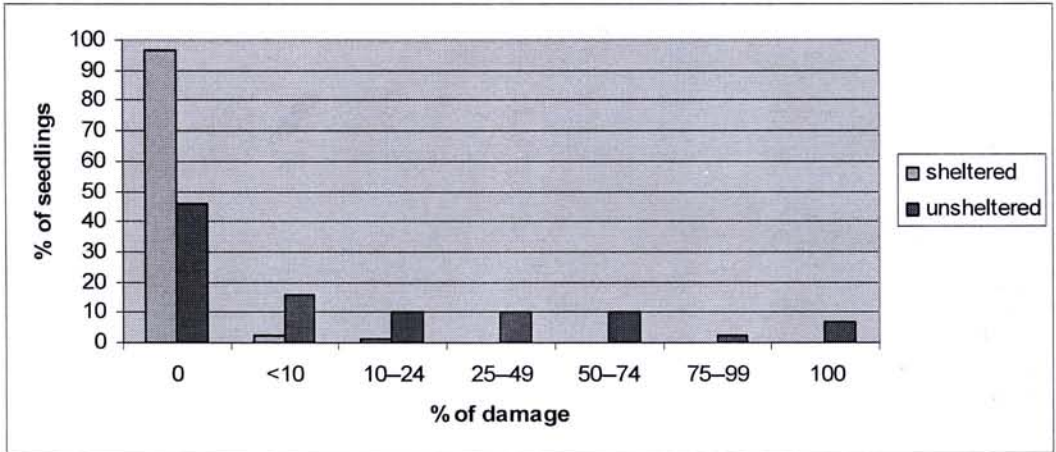


Figure 4. Percentage of *Pinus uncinata* seedlings with various proportions of dead leaves after the first winter in the treeline ecotone, according to the nurse effect from *Rhododendron* shrubs (n = 96 at each position, sheltered vs. unsheltered).

CONCLUDING REMARKS

In short, regeneration of *Pinus uncinata* above the timberline is subject to a wide range of impediments. The scarcity of seedlings beyond the treeline ecotone suggests dissemination shortness, and that emergence, survival and growth are impeded by harsh winter conditions in open pasture. In this ecotone the irregular vegetation structure provides safe microsites and good light conditions for seeds that arrive from the neighbouring forest. These regeneration microsites are flat or slightly concave surfaces at the lee edge of shrubs and krummholz. Seedlings that emerge in any other position are doomed to suffer the harsh effects of winter for their first few years. Sheltered seedlings will also encounter harsh conditions as they grow into saplings, as leader shoots become unprotected by the remaining snow (Figure 5). Thus, even regeneration in favourable microsites depends on periods of a few favourable consecutive years: mild winters and long growing seasons. This may be the only climatic scenario in which saplings may escape from the strongest effects of winter desiccation.

Ongoing experiments on the performance of seedlings and saplings may help us to understand the limitations of *Pinus uncinata* regeneration beyond the timberline, and also the climatic aspects responsible of the observed slow or unappreciable upward advance of this forest border.



Figure 5. Scarce krummholz individuals of *Pinus uncinata* succeed in forming vigorous leader shoots, which sometimes show a 'empty zone' at the height where snow abrasive effects are harsher.

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