A Simple Spatial Model Exploring Positive Feedbacks at Tropical Alpine Treelines

Authors: Bader, Maaike Y., Rietkerk, Max, and Bregt, Arnold K.

Source: Arctic, Antarctic, and Alpine Research, 40(2) : 269-278

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(07-024)[BADER]2.0.CO;2

Arctic, Antarctic, and Alpine Research, Vol. 40, No. 2, 2008, pp. 269–278

A Simple Spatial Model Exploring Positive Feedbacks at Tropical Alpine Treelines

Maaike Y. Bader[*‡]*
Max Rietkerk[†] *and*
Arnold K. Bregt[*]

[*]Centre for Geo-information,
Wageningen University, P.O. Box 47,
6700 AA Wageningen, The Netherlands
[†]Department of Environmental
Sciences, Copernicus Institute, Utrecht
University, P.O. Box 80115, 3508 TC
Utrecht, The Netherlands
[‡]Corresponding author. Present
address: Department of Biology and
Environmental Sciences, Functional
Ecology of Plants, University of
Oldenburg, D-26111 Oldenburg,
Germany
maaike.bader@uni-oldenburg.de

Abstract

Climate change could cause alpine treelines to shift in altitude or to change their spatial pattern, but little is known about the drivers of treeline dynamics and patterning. The position and patterns of tropical alpine treelines are generally attributed to land use, especially burning. Species interactions, in particular facilitation through shading, may also be important for treeline patterning and dynamics. We studied how fire in alpine vegetation and shade dependence of trees may affect the position and spatial pattern of tropical alpine treelines and their response to climatic warming, using a spatial minimal model of tree growth at treeline. Neighboring trees provided shade and protection from fire. The positive feedback that resulted from these neighbor interactions strongly affected the emergent treelines and always reduced the distance and speed of treeline advance after a temperature increase. Our model demonstrated that next to fire, shade dependence of trees can also lead to abrupt treelines and relatively low treeline positions. This implies that these patterns do not necessarily indicate human disturbance. Strong abruptness of a treeline may indicate that it will respond slowly to climatic changes.

DOI: 10.1657/1523-0430(07-024)[BADER]2.0.CO;2

Introduction

Alpine treelines are largely climate dependent, so climatic changes could cause changes in treeline altitude or spatial patterns. Various properties of treelines make the rate and direction of such changes difficult to predict. These include the presence of land use and other disturbances, interactive effects of different climatic factors, topographic complexity, slow reactions due to slow demographic processes, and complex dynamics due to positive feedbacks between vegetation and microclimate (Slayter and Noble, 1992; Noble, 1993; Kupfer and Cairns, 1996; Malanson, 2001; Graumlich et al., 2004; Holtmeier and Broll, 2005). None of these properties are well understood, not in temperate regions and even less so in the tropics.

We will focus here on the complex dynamics that may arise from positive feedback. Positive feedback affects not only treeline dynamics but also the spatial pattern of the treeline ecotone (Wilson and Agnew, 1992; Smith et al., 2003; Resler, 2006). Existing treeline patterns include abrupt boundaries, gradual transitions, and vegetation mosaics (Wardle, 1965; Körner, 1998; Camarero et al., 2000). These patterns are often not related to patterns in substrate or topography, but can be brought about by plant interactions alone (Armand, 1992; Wilson and Agnew, 1992). Being able to interpret these patterns in terms of underlying processes is important both for understanding treeline ecology and for predicting the response of treelines to climatic changes (Wiegand et al., 2006).

Simple mechanistic spatial models have an important potential for studying the effect of local interactions on emergent spatio-temporal patterns (Rietkerk et al., 2002). Previous treeline models of this type have focused on coniferous species in temperate regions (Malanson, 1997, 2001; Alftine and Malanson, 2004; Wiegand et al., 2006), and the results probably cannot be extrapolated to tropical treelines, or even to many other temperate treelines. For instance, in the model by Alftine and Malanson (2004) wind and snow are important factors, while at tropical treelines they do not play significant roles (Sarmiento, 1986). In the model by Wiegand et al. (2006) the trees are shade intolerant, while tropical treeline species are often shade dependent (Bader et al., 2007b). Positive feedback has also been modeled generically as a positive effect of neighbors on site conditions (Malanson, 1997, 2001).

Our study focuses on the vegetation dynamics and spatial patterns of tropical alpine treelines, defined as the transition between upper montane cloud forest and páramo, the latter in the broad sense of tropical alpine vegetation (Hofstede et al., 2003). In tropical mountains solar radiation can reach very high intensities due to the high sun angle and thin atmosphere layer (Caldwell et al., 1980). Although sunlight is a resource for plants, excess radiation can cause a decrease of photosynthetic potential and damage to plant tissues (Barber and Andersson, 1992; Long et al., 1994). This photoinhibition, the negative effect of excess radiation, is stronger at low temperatures (Ball et al., 1991; Krause, 1994; Huner et al., 1998; Close et al., 2000), especially if there is a frost. Frosts can occur nightly in tropical alpine areas, which are characterized by strong diurnal, rather than seasonal, temperature fluctuations (Sarmiento, 1986; Rundel, 1994). Tree seedlings at several treelines, both tropical and temperate, have been found to be shade dependent and sensitive to cold-induced photoinhibition (Wardle, 1965, 1985; Ball et al., 1991; Germino and Smith, 1999; Bader et al., 2007b).

Natural treelines are largely climate controlled, but natural treelines are rare, especially in the tropics (Miehe and Miehe, 1994). Here, most areas above the actual treeline are used for livestock grazing in combination with fire management, and these fires commonly play an important role in the vegetation dynamics (Hofstede et al., 1995; Suarez R. and Medina, 2001). Although fire usually does not spread into the moist cloud forest, it can strongly influence treeline patterns and dynamics, especially by removing

1523-0430/08 $7.00

young trees that may emerge in the páramo above the actual treeline. Many tropical treelines may have been lowered by fire and may continue to be influenced by it (Laegaard, 1992; Miehe and Miehe, 1994).

We present a minimal model of tree growth at the tropical alpine treeline, addressing the effects of shade dependence of trees and the effects of fire in the páramo. By using a minimal modeling approach we did not aim at completeness through the incorporation of all biological detail, nor did we aim at quantitative predictions. Instead, we aimed at a qualitative assessment of the type of patterns and dynamics that can emerge as a result of positive feedback processes. In the model, solar radiation and fire are drivers of positive feedback switches (Wilson and Agnew, 1992). Such a switch occurs when a vegetation type alters the environmental conditions such that it favors itself relative to other vegetation types, which can cause a sharpening of boundaries and the emergence of stable vegetation mosaics. The model is explicitly spatial; trees receive shade and protection from fire from neighboring trees. The model demonstrates the effects of these local interactions on treeline spatial patterns, dynamics, and the response to warming.

Methods

MODEL STRUCTURE

The model represents the growth of trees in a 2-dimensional grid. Each grid cell represents an area of about 2 × 2 m, and the state variable of each grid cell is tree height. This simplifies trees to square columns, which in this paper we will refer to as 'trees.' Tree growth follows a logistic function and is reduced at high radiation with low minimum temperature by reduction factor p.

$$\frac{\mathrm{dH}}{\mathrm{dt}} = \mathrm{p}\cdot\mathrm{r}\cdot\mathrm{H}\cdot\frac{\mathrm{H_{max}} - \mathrm{H}}{\mathrm{H_{max}}} - \mathrm{d}\cdot\mathrm{H} \qquad (1)$$

where t = time (months); H = tree height (m); p = growth reduction factor ($\leq$1), which is a function of radiation (R) (Equation 2); r = specific growth rate (month^{-1}); $H_{\max}$ = the maximum tree height if $d = 0$ (m); and d = loss rate (month^{-1}).

Reduction factor p represents the fraction of the maximum carbon assimilation (photosynthesis – respiration) that is being reached (Fig. 1) and is calculated by a hyperbolic photosynthetic response curve (Landsberg, 1986; Spitters, 1986), as follows:

$$\mathrm{p} = \frac{\mathrm{q}\cdot\mathrm{R}\cdot\mathrm{mp}}{\mathrm{q}\cdot\mathrm{R} + \mathrm{mp}} - \mathrm{resp} \qquad (2)$$

where mp = maximum photosynthesis level (0–1), which is less than 1 under photoinhibition, as a function of radiation (Equation 3); q = the quantum yield (efficiency) or initial slope of the photosynthetic response curve (Watt^{-1} m^{2}); R = radiation level received by the tree (Watt m^{-2}); and $resp$ = respiration (0–1).

The maximum photosynthesis level (mp) decreases linearly under high radiation levels due to photoinhibition. The following equation is based on graphs sketched in Falowski et al. (1994) and Huisman (1997):

$$\mathrm{mp} = 1 - \frac{\mathrm{R} - (\mathrm{R_s} - \mathrm{rt}\cdot\mathrm{T})}{\mathrm{R_m} - \mathrm{R_s}} \qquad (3)$$

where R_s = radiation level at which photoinhibition starts (Watt m^{-2}); rt = lowering of R_s for each degree of lower minimum air temperature (Watt m^{-2} °C^{-1}); T = minimum air temperature (°C); and R_m = radiation level above which photoinhibition is maximal (so photosynthesis is 0) (Watt m^{-2}). Shade dependence is expressed as the relative advantage of trees in the shade compared to trees exposed to radiation. It can be increased by lowering the radiation tolerance of the trees by lowering R_m, or by increasing the amount of shade provided by neighbors.

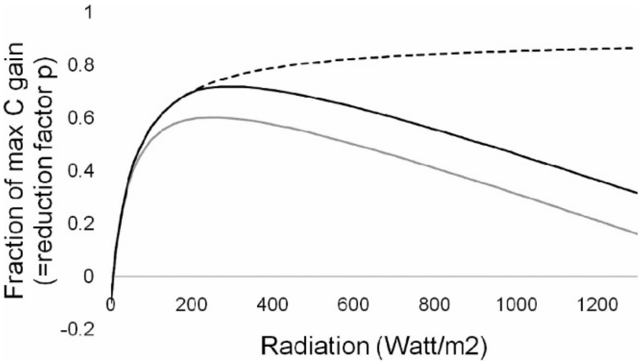

FIGURE 1. Reduction factor p as a function of radiation. The dashed line indicates the potential carbon gain if no photoinhibition would occur, i.e. with mp = 1. The gray and the black lines indicate the potential carbon gain with photoinhibition, whereby the gray line shows the additional negative effect of a low minimum temperature (−10°C, versus 2°C in the black line).

Radiation is decreased as a function of the size of the trees in the eight neighbor cells. For simplicity, we assume that temperature is not affected by neighbors. The radiation strength in the shade of neighbors is calculated using Lambert-Beer's law:

$$\mathrm{R} = \mathrm{R_{ext}}\cdot\exp\left(-\mathrm{k}\cdot\sum \mathrm{w_{ij}}\cdot\frac{\mathrm{H_{ij}}}{\mathrm{H_m}}\right) \quad \mathrm{i, j} = -1,0,1 \qquad (4)$$

where R_{ext} = external radiation (radiation in the absence of neighbors) (Watt m^{-2}); k = extinction coefficient for radiation in the canopy (–); H_m = maximum tree height actually reached in the model ($< H_{\max}$ if $d > 0$) (m); H_{ij} = height of neighbor trees (direct and diagonal) (m); w_{ij} = weight factor (0–1); and i and j indicate the positions of neighboring cells.

It is explicitly assumed that all space not occupied by trees is occupied by tussock grass páramo and that small tree seedlings are omnipresent in the grass layer. Dispersal limitation may occur at real treelines (Dullinger et al., 2004), but the purpose of our model was specifically to explore the effects of radiation and fire only. Tree seedlings emerge from the grass layer when the conditions of radiation and minimum temperature are more favorable than a fixed threshold: $R - (R_s - rt\cdot T) < R_e$, where R_e = radiation threshold for seedling establishment (Watt m^{-2}). This threshold is lower than the equilibrium threshold for tree growth based on the model equations, i.e. seedling emergence is more sensitive to radiation than tree growth. Trees get established with a starting size of 0.5 m, which is the assumed height of the grass layer.

The páramo grass tussocks, which contain a high fraction of dead standing biomass, are good fuel, and fire periodically damages trees that have too many grass neighbors (>4). Trees less than 2 m tall are removed completely by fire, while larger trees are reduced by $1/H$ at each fire event. The model is fully deterministic.

SIMULATIONS

The model was run on a 100*100 cell grid. Minimum temperature decreased linearly from the bottom to the top of the grid, while external radiation was uniform in space. This imitates the relatively small rates of increase of radiation with altitude compared to the lapse rate of temperature. The initial tree

TABLE 1

Elements of the model.

Symbol	Description	Units	Values used	References
t	time	months	variable	
T	minimum temperature	°C	ca. –10 to 2	Rundel (1994)
R_{ext}	external radiation	Watt m^{-2}	1300 (var. in Fig. 2)	Körner (1999)
R	radiation received by tree	Watt m^{-2}	variable	
H	tree height	m	variable	
H_{max}	maximum tree height if $d = 0$	m	30	personal observation
r	tree growth rate	m m^{-1} month^{-1}	0.03	calibrated
d	tree death rate	m m^{-1} month^{-1}	0.006	calibrated
p	growth reduction factor	≤ 1	variable	
q	initial slope photosynthetic response curve	Watt^{-1} m^{2}	0.02	calibrated
$Resp$	Respiration	0–1	0.1	calibrated
R_{s}	radiation level start of photoinhibition	Watt m^{-2}	100 (800 in Fig. 3)	Egerton et al. (2000)
R_{m}	radiation level maximum photoinhibition	Watt m^{-2}	2000 (var. in Fig. 3)	calibrated
R_{e}	upper radiation threshold for establishment	Watt m^{-2}	1300	calibrated
rt	change in R_{m} for each degree $T < 2$°C	Watt m^{-2} $°\mathrm{C}^{-1}$	-25	calibrated
k	extinction coefficient radiation in canopy	—	0 to 0.8	Landsberg (1986}
w	weight factor for shading from neighbors	—	1 or 0.7*	

* Weighted by distance: 1 for direct neighbors, 0.7 for diagonal neighbors.

pattern was a linear gradient from 0% cover at the lowest minimum temperature (top row of the grid) to 100% cover at the highest minimum temperature (bottom row of the grid). The initial pattern was identical for sets of model runs that are presented together for comparison. As boundary conditions, we assumed that there were no trees above the top end of the grid and a full cover of 10-m- tall trees below the bottom end, while the left and the right ends were connected, so that the grid was cylindrical.

The parameter values used for constants and inputs are given in Table 1. These values were based on realistic values from literature when possible, while others were calibrated to make the model run within realistic bounds. The exact values of these parameters did not affect the qualitative effects of each of the different feedback scenarios, so they were of limited relevance to the purpose of our study. Other parameters were varied; this constituted the different feedback scenarios.

To study the effect of climatic warming on our modeled treeline, we increased the minimum temperature by 3.6°C over one year or over 100 years. The one-year scenario was added to facilitate the interpretation of the dynamics after change; there was no qualitative difference in the response to this abrupt change or to the more gradual change. The 100-year scenario is in the range of estimates for global temperature increase over the next 100 years (IPCC, 2007; Stainforth et al., 2005). The model was run for 800 years, to allow a stabilization of the treeline before and after the rise in temperature.

The result of the modeled interactions with neighbors is a positive feedback: trees locally promote the establishment and growth of trees, while páramo (or the absence of trees) locally inhibits the survival and growth of trees and thereby promotes páramo. The strength of this positive feedback is determined by the relative advantage of trees neighboring other trees compared to trees neighboring páramo. Having too many very large neighbors constitutes a disadvantage, because light levels may become too low (see Fig. 1). This theoretically results in negative feedback. However, for this to play a role in the model, a small tree would have to be surrounded on all sides by large trees. This does not occur because, due to the positive feedback, such a tree would have grown large before its neighbors became so large that they negatively affect its growth. And for large trees the negative feedback only restricts the maximum size reached, but not persistence.

We varied the strength of the positive feedback in three ways: (1) through the amount of shade produced by trees (varying k); (2) through the radiation tolerance of trees (varying R_{m}); and (3) through the addition of fire events (every 5 years). The first two parameters both affect the feedback loop driven by excess radiation, while fire adds a new feedback loop (Fig. 2).

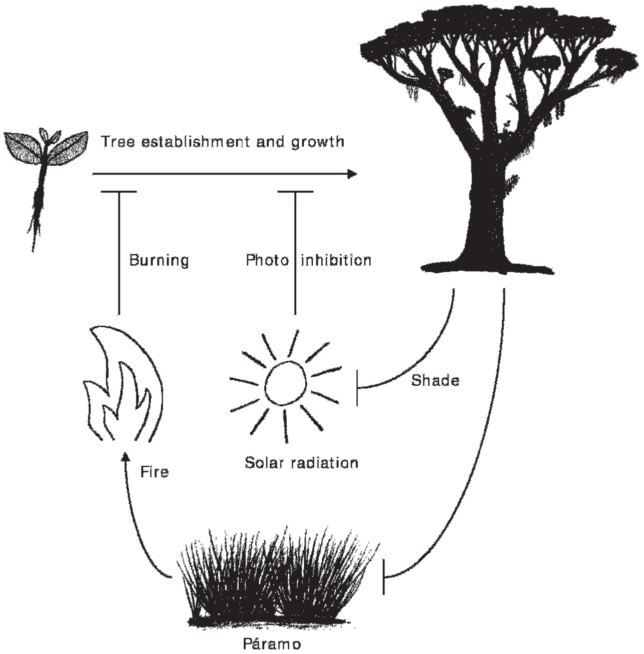

FIGURE 2. Positive feedback loops present in the model. Stopping symbols ($\top$) indicate inhibitory effects, arrows indicate promotory effects. The inner loop shows positive feedback mediated by excess radiation, the outer loop shows positive feedback mediated by fire. Trees positively influence tree growth and establishment by providing shade, thereby lowering the intensity of solar radiation and thereby limiting photoinhibition. In the model the presence of a tree also implies the absence of páramo tussock grasses, so that trees restrict fire and hence positively influence tree growth and establishment.

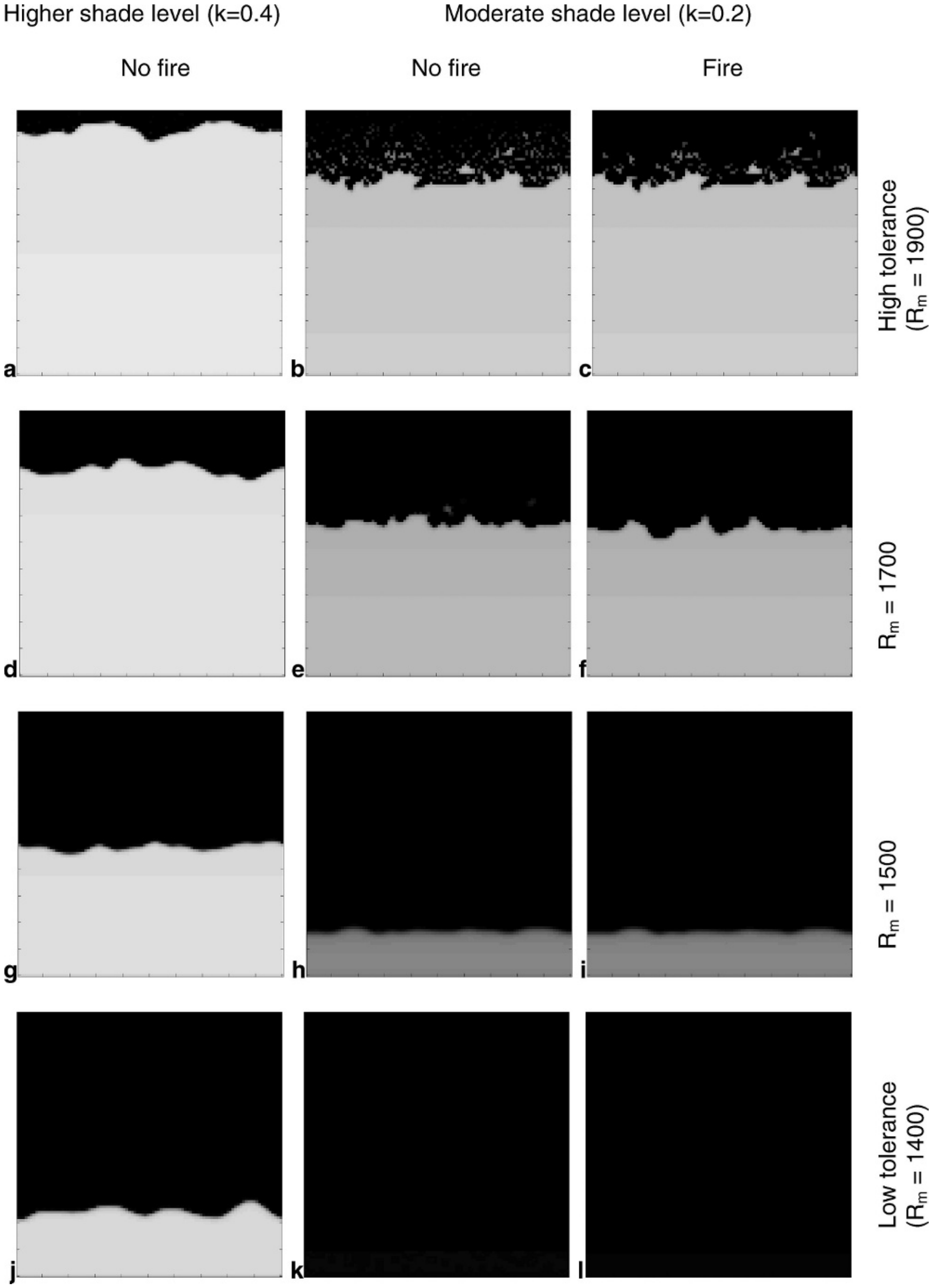

FIGURE 3. Effects of radiation tolerance, shade from neighboring trees, and fire on the position and the pattern of the treeline. Shown are spatial patterns of tree height after running the model for 800 years. Radiation tolerance decreases from the top to the bottom row: $R_m = 1900$, 1700, 1500, and 1400 Wm^{-2} (decreasing tolerance); R_s = 800 Wm^{-2}; R_{ext} = 1300 Wm^{-2}. Trees provided more shade in the left column (k = 0.4) than in the middle and right column ($k = 0.2$). In the left and middle columns there was no fire, while in the right column there were fires every 5 years. Temperature did not change through time. The grid size is 100 × 100 cells. The initial pattern was exactly the same for each run, and was a randomly assigned linearly decreasing cover of 10-m-high trees, from 100% cover (bottom of grid) to 0% cover (top of grid). Gray shades indicate tree height, ranging from 0 (black) to 24 m (white).

To emphasize that the temperature gradient represents a gradient related to altitude, we refer to positions on this gradient in terms of altitude: a lower temperature corresponds to a higher altitude. The 'altitudinal' boundary zone between continuous areas of trees (forest) and continuous areas where trees are absent (páramo) represents the treeline. Treeline dissectedness is the length of boundary between trees and non-trees, and includes patchiness. Treeline abruptness is the rate of increase in tree height along the slope at the treeline, scaled between zero and the maximum attained tree height.

Results

Running the model on a temperature gradient resulted in the emergence of a treeline, unless the settings for shade, radiation tolerance, and fire frequency were such that the treeline was situated outside the range of the gradient (Fig. 3). This was the case, for instance, if the radiation tolerance was too low relative to the external radiation and the strength of shade provided by neighbors (Figs. 3k and 3l). The position, spatial pattern, and dynamics of the treeline were strongly altered by positive feedback and varied according to the settings for shade, radiation tolerance, and fire.

TREELINE POSITION AND PATTERN

With increasing shade from neighbors, the treeline was situated at higher altitudes and the spatial pattern of treeline was less dissected (Fig. 3). If trees were less tolerant to radiation, the treeline was situated at lower altitudes and its spatial pattern was again less dissected. Finally, fire caused a slight depression of treeline altitude and lower dissectedness. The effect of fire on treeline dissectedness was especially evident at low shade levels, where fire removed single trees and small patches (Figs. 3c and

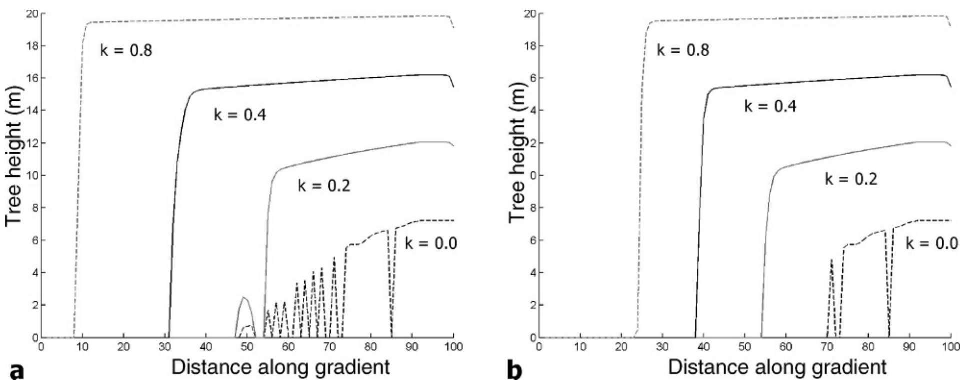

FIGURE 4. The effect of shade and fire on the abruptness of the treeline transition: Tree height along a transect from the top to the bottom of the grid after running the model for 800 years. The transect is the 50th column of the grids shown in the left columns of Figures 7a and 8b. (a) Scenarios without fire. (b) Scenarios with fire occurring every 5 years. In both graphs the lines represent different shade levels: no shade ($k = 0$), intermediate shade ($k = 0.2$, $k = 0.4$), and strong shade ($k = 0.8$). Note how both shade and fire increase the abruptness of the transition.

3f). At higher shade levels treeline dissectedness was low anyway, due to the effects of shade. The abruptness of the treeline is also affected by fire mainly at the lowest shade levels (compare Fig. 4b to Fig. 4a), where it makes the treeline more abrupt by removing the smallest (single) trees.

Shade increased the abruptness of the treeline, especially when we compared low levels of shade to no shade (Fig. 4). In line with this, if there was shade, treelines were abrupt at all levels of radiation tolerance (Fig. 5). At low shade levels, decreased radiation tolerance resulted in smaller trees (Fig. 5a) and a slightly more gradual treeline, but at higher shade levels (Fig. 5b) this effect largely disappeared.

When the model was run without neighbor interactions (no shade) and without fire, so without positive feedback, tree height gradually decreased with altitude, reflecting the temperature gradient (Figs. 4a and 7a). The patchiness of this treeline reflects the initial pattern used for the model run and the impossibility of new tree establishment above the externally determined threshold altitude.

TREELINE DYNAMICS

In scenarios without warming, treeline positions moved slowly towards an asymptote after the quick cover increase or decrease in the period following initialization of the model (Fig. 6). All lines in Figure 6 originate at 50% cover. In the first time-step of the simulation (the first month), tree cover increased rapidly in the runs with the most radiation tolerant trees (Fig. 6a) and in those with shade (Fig. 6b), because seedlings could establish in all locations favorable enough at that time. These favorable locations included all open sites below the altitudinal establishment limit plus all open sites with enough tree neighbors. Such fast seedling establishment also caused the jump in cover at the time of warming; at this time a number of sites suddenly became just favorable enough for establishment.

Treeline advance after warming was also slowed down and limited in extent by stronger shade (Figs. 6b and 7). The jump in cover at the time of warming was especially large in the scenario without shade, because in this scenario trees were solely dependent

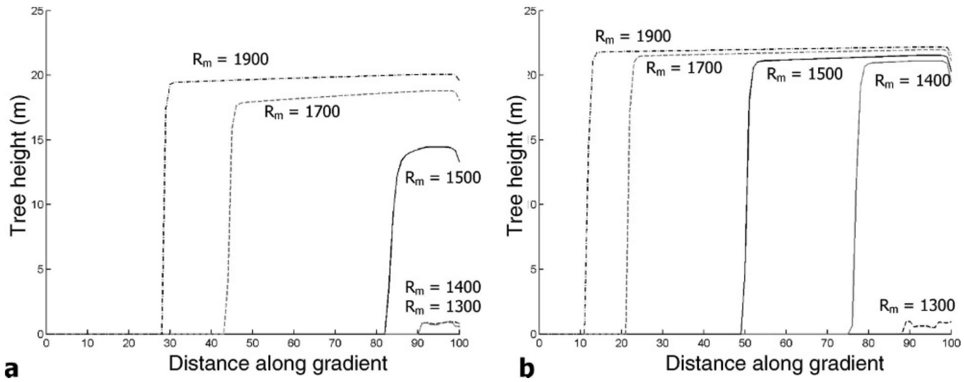

FIGURE 5. The effect of radiation tolerance and shade on the abruptness of the treeline transition: Cross sections of tree height along transect from the top (0) to the bottom (100) of the grid after running the model for 800 years. The transects are the 50th column of the grids shown in the middle (a) and left (b) columns of Figure 3. (a) Scenarios with $k = 0.2$. (b) Scenarios with $k = 0.4$. In both graphs the lines represent different radiation tolerance levels, from high ($R_m = 1900$ Wm^{-2}) to low ($R_m = 1300$ Wm^{-2}) tolerance. Other parameter settings: $R_s = 800$ Wm^{-2}, and $R_{ext} = 1300$ Wm^{-2}. The lowest tolerance did not allow any tree growth, only the continuous replacement of emerging seedlings. The height decrease at the right of each graph (position 100) is due to the boundary condition: 10-m-high trees below the bottom row of the grid. This condition did not affect treeline properties.

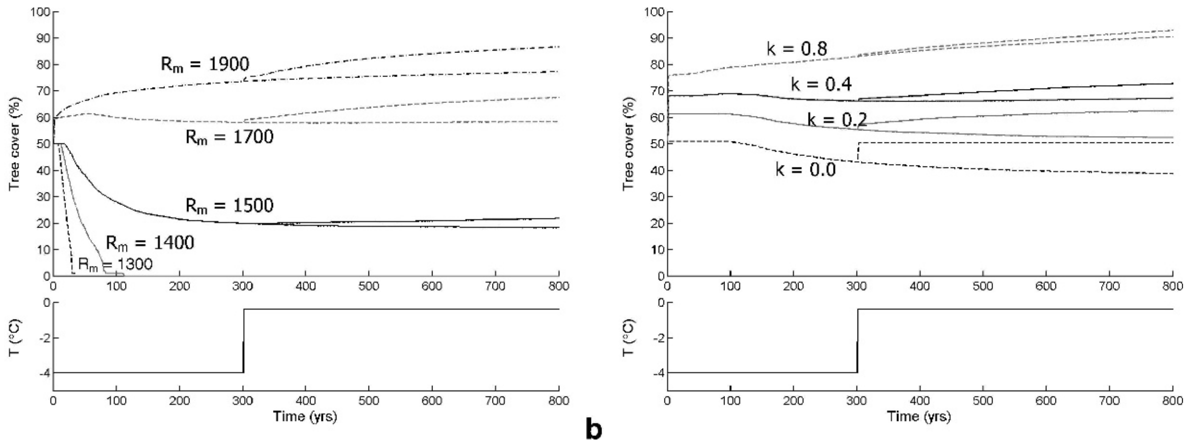

FIGURE 6. Tree cover with constant and with abruptly increased temperature. Temperature change of the central cell of the grid is shown in the bottom graphs. All are scenarios without fire. Starting cover is 50% in all cases—quick cover increase in the first year is due to quick establishment in all sufficiently favored sites. (a) Effect of radiation tolerance, from high to low tolerance. Same runs as in the middle column of Figure 3 ($k = 0.2$). (b) Effect of the shade level. Same runs as those in Figure 7. Note how both stronger shade and low radiation tolerance decrease the reaction to temperature increase.

on the external climate, and a rise in temperature caused a rise in the establishment limit and subsequent quick seedling establishment. If shade played a role, the treeline could be situated above the external establishment limit, and a rise in temperature only increased establishment in some shaded sites. After the initial jump, cover increase was highest with light shade; without any shade new establishments above the external limit were impossible and further advance depended on the recovery of suppressed trees, while stronger shade allowed the treeline to be situated at higher altitudes even under the pre-warming conditions, and rendered it increasingly insensitive to changes in the external temperature gradient.

Figures 7 and 8 show the increase in tree cover (independent of tree height) due to warming. The strange pattern of change in Figure 7c can be explained as follows: the bottom patterned area reflects the filling in of gaps due to a rise of the establishment limit, the black band is where trees persisted both with and without a rise in temperature, and the top patterned area shows trees that persisted only if there was a rise in temperature.

Fire strongly slowed down and limited the upward shift of the treeline after warming (compare Figs. 7 and 8). This was due to the fact that isolated trees or small patches of trees above treeline had been removed (burned), and due to continued burning of seedlings emerging above the treeline. Without fire and with no or weak shade, patches and single trees had remained, more or less suppressed in stature, above the closed treeline (Figs. 7a and 7d). These suppressed trees could react quickly to warming through increased growth. Where fire had removed these isolated trees and patches, establishment was only possible in the shaded cells just above the existing closed treeline, and treeline advance was slower and limited in extent.

Discussion

The position, spatial patterns, and dynamics of the treeline were all affected by positive feedback, but the effects differed depending on which parameters were used to strengthen the positive feedback switch. If the switch resulted from stronger shade, treelines were positioned at higher elevations, while if the switch resulted from lower radiation tolerance or from fire, treelines were positioned at lower elevations. Stronger shade or fire made the treeline less dissected and more abrupt, while lower radiation tolerance also made the treeline less dissected, but not more abrupt. The advance of the treeline after a temperature increase was always reduced in speed and extent by a stronger positive feedback switch, whether it be brought about by stronger shade, lower radiation tolerance, or fire.

So, the overall negative effects of lower radiation tolerance and fire caused lower treelines and slowed down and limited treeline advance after the temperature increase. However, the overall positive effect of stronger shade caused higher treelines but also slowed down and limited treeline advance. It is clear that the observed effects on the reaction of the treeline to climate change are not the result of an overall positive or negative effect on tree growth, but of a positive feedback switch that stabilizes the treeline. The strongest stabilization is achieved by the combination of shade and fire, causing a two-factor switch (Wilson and Agnew, 1992).

For a quantitative prediction of a treeline's response to climatic change, a model should include several additional processes, especially dispersal (vegetative or through seeds) and interactions with the alpine vegetation (Malanson, 1997; Dullinger et al., 2004). Dispersal limitation and competition from alpine vegetation could strongly slow down forest expansion and would, for instance, limit the fast forest cover increase observed at the initiation of our model and after warming. However, our model was not aimed at quantitative predictions; for such predictions a different model structure is needed, as well as extensive field research for obtaining realistic estimations for all parameters (Dullinger et al., 2004). More importantly, the importance and functioning of all relevant processes needs to be well understood, which they are not for tropical alpine treelines, or indeed alpine treelines in general.

The reason that a positive feedback switch limits and slows down forest extension is that it makes trees depend more on neighbor interaction and less on the external climate; in other words, the treeline gets partly uncoupled from the external climate. If feedback plays no or a small role, a treeline will be located more or less where the external environment dictates it to be, and under these circumstances a change in this external environment can have a direct effect on treeline position. However, protection by neighbors allows trees to grow where the external environment is unsuitable for growth—in other words, mutual facilitation allows trees to grow beyond their

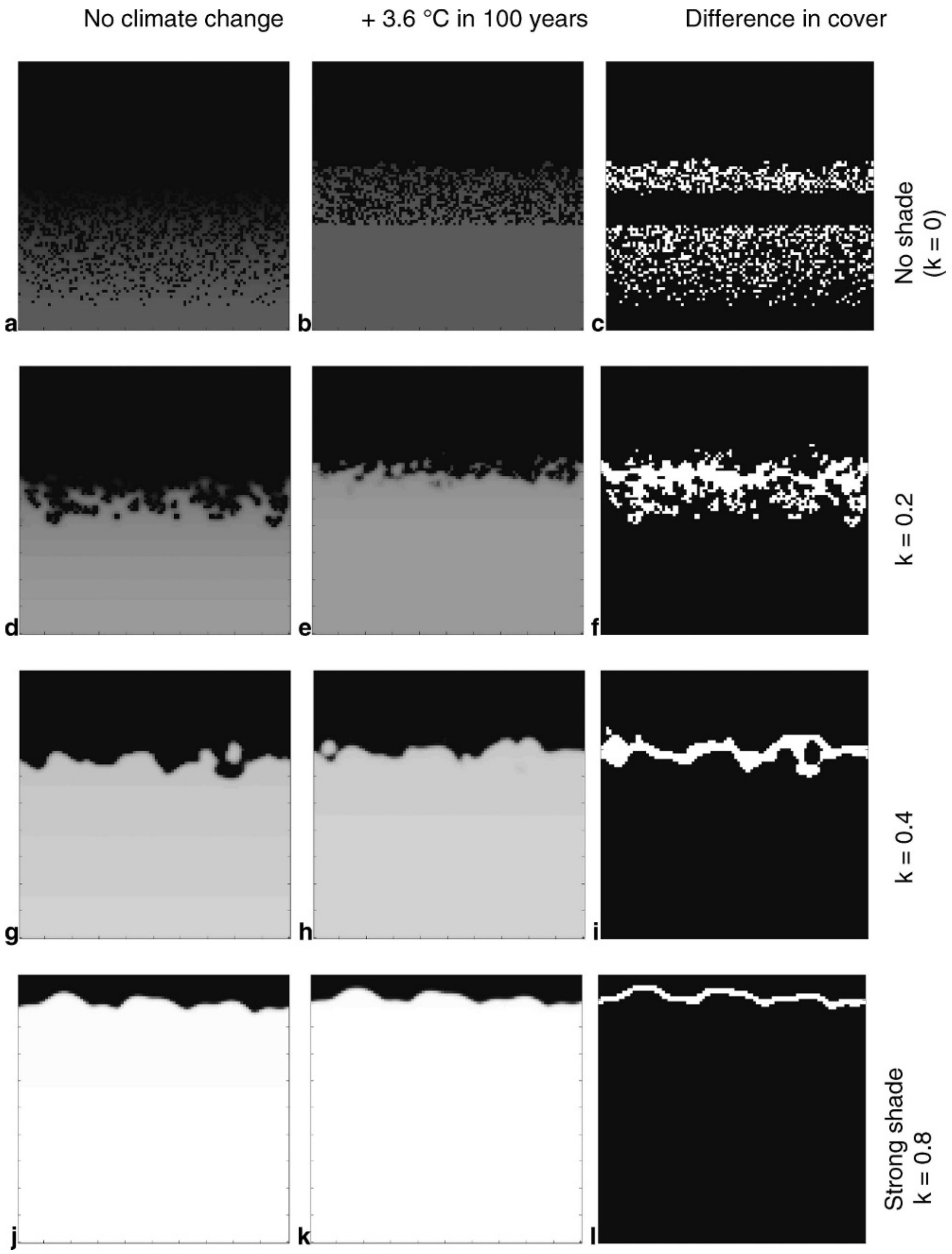

FIGURE 7. Effects of climate change on final pattern of treelines without fire and with different levels of shade from neighbors. Shown are spatial patterns of tree height after running the model for 800 years. The grid size is 100 × 100 cells. The initial pattern was exactly the same for each run, as well as for those in Figure 8, and was a randomly assigned linearly decreasing cover of 10-m-high trees, from 100% cover (bottom of grid) to 0% cover (top of grid). Each row of images represents a different level of shade from neighboring trees, which has a positive effect on tree growth. The left column shows the result if the temperature gradient is kept constant throughout the 800 years. The middle column shows the result if temperature is increased by 3.6°C over 100 years (between year 300 and 400), and the right column shows the increase in tree cover (in white) due to this increase in temperature. The black band in Figure 7c represents a zone where trees have persisted both with and without warming. In the first two columns gray shades indicate tree height, ranging from 0 (black) to 20 m (white).

'fundamental niche' (Bruno et al., 2003). Even if this external environment improves by a rise in temperature, growth outside the protection of neighbors is still impossible, so that treeline advance is limited. In contrast, if the external environment deteriorates, growth may still be possible within the protection of neighbors, so treeline retreat will also be limited. Positive feedback thus buffers the treeline against external changes and causes hysteresis: a change from forest to páramo will occur at lower external temperatures than a change from páramo to forest (Armand, 1985, 1992).

This hysteresis implies a strong dependence of treeline position on its own history. In the model this was reflected in the effect of the initial pattern of trees on the final position of the treeline (not shown); a higher initial tree density led to treelines at higher altitudes if positive feedback occurred. The 'climatic' treeline is therefore a difficult concept, and does not relate to the actual position of existent treelines, including natural treelines. Instead, there is an altitudinal zone, which may be several hundreds of meters wide, where both forest and páramo are natural vegetation types, representing alternative system states.

The existence of such alternative states implies that shifts from one state to the other occur 'catastrophically,' as an accelerated change once a threshold in external conditions is reached or due to a disturbance (Rietkerk and van de Koppel, 1997; Scheffer et al., 2001; Scheffer and Carpenter, 2003; Rietkerk et al., 2004). In our model such accelerated shifts did not occur, because the threshold temperature for tree establishment without the shade of neighbors was not reached in the warming scenarios. The limited advance due to positive feedback can be considered as pre-catastrophic inertness to change.

Malanson (1997, 2001) increased positive feedback in his treeline model by increasing the positive effect of neighbors on a compound 'site quality.' Similar to our results, positive feedback resulted in more abrupt treelines (Malanson, 1997). However, in contrast to our results, positive feedback resulted in a quicker forest cover increase after climatic change (Malanson, 2001). This was the result of the overall positive effect of the presence of trees. We also found that a stronger positive effect, i.e. stronger shade, caused quicker forest cover increase, but only at the initiation of the model runs, so starting from a

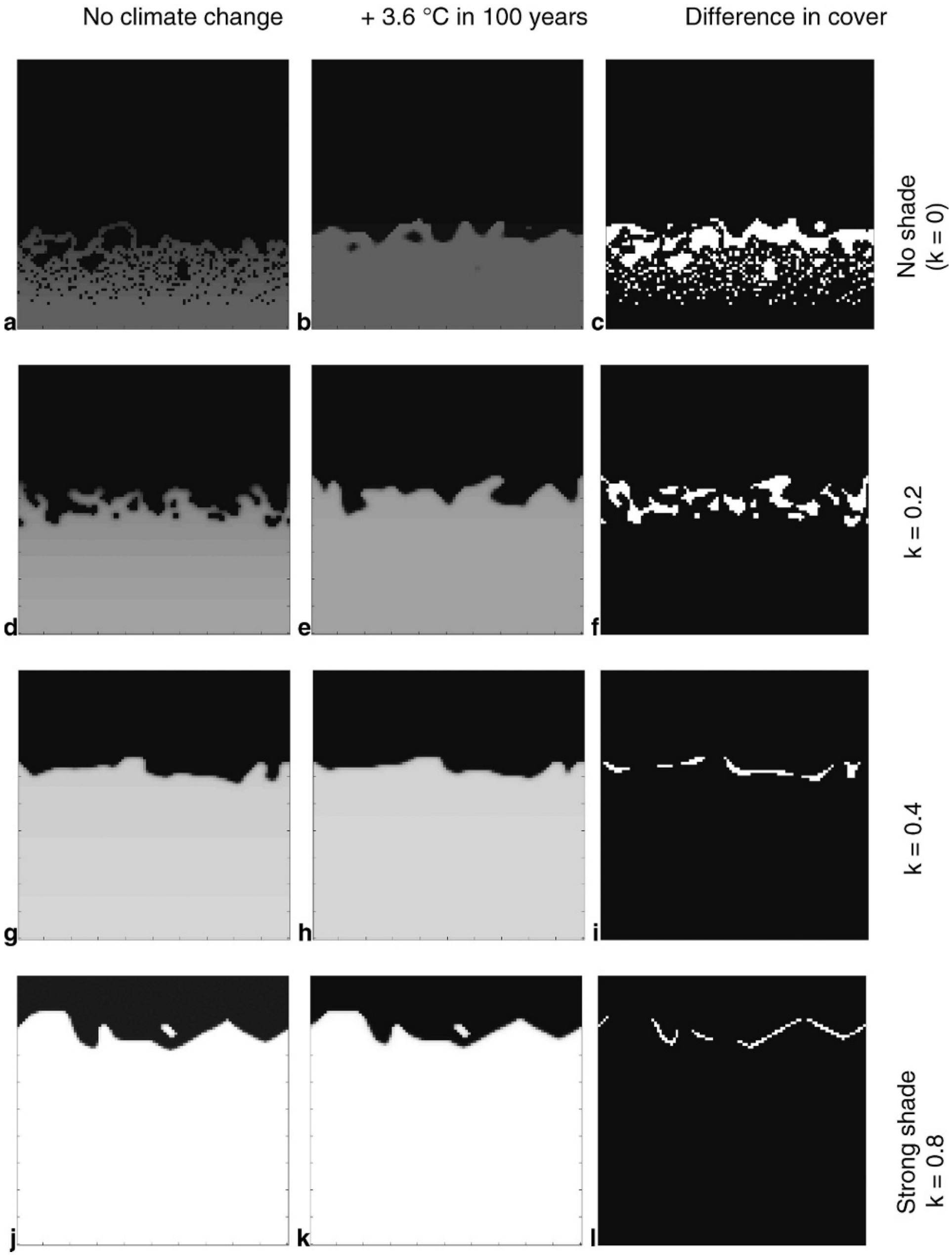

FIGURE 8. Effects of climate change on final pattern of treelines with fire occurring every 5 years. For further details see caption for Figure 7.

situation far from equilibrium. If the temperature was increased when the treeline was in a more or less stable position, stronger shade (positive effect) as well as lower radiation tolerance and fire (negative effects) slowed down and limited forest extension. This shows the importance of understanding the history and current dynamics of a treeline in order to predict its reaction to climatic change.

Increasing the positive effect of trees on neighbors, in our case by increasing the amount of shade, is the easiest way of strengthening the positive feedback switch in a model such as ours or that of Malanson (1997, 2001). However, differences in switch strengths between different treelines in the field will more likely be related to the radiation tolerance of the tree species rather than the amount of shade produced. Our results show that stronger shade and lower radiation tolerance have opposite effects on treeline position, though both result in a stronger switch. Stronger shade increases the positive effect of having tree neighbors so that patches expand and merge and the treeline will lie above the climatic boundary for individual trees. In contrast, lower radiation tolerance causes a lowering of the climatic boundary for individual trees, which increases the negative effect of having non-tree neighbors so that single trees and small patches disappear. The effect of fire is different: a higher fire frequency also increases the negative effect of having non-tree neighbors, but the result is that the treeline lies below the climatic boundary for individual trees. Therefore, a treeline that is affected by fire may move upwards at cessation of burning, while it reacts little to a change in climate.

Positive feedback can cause abrupt treelines, but a recent treeline model by Wiegand et al. (2006) shows that treelines with abrupt height transitions can emerge without positive feedback due to certain combinations of demographic parameters. However, the necessary parameters (seedling mortality rising rapidly with altitude, mortality dropping rapidly with age, and little growth inhibition) do actually imply a positive feedback: once a tree is established it grows well and its chance of mortality drops fast, while if no tree is established it is unlikely that it will, due to high seedling mortality. In our model a similar effect occurs, because seedling establishment is more sensitive to radiation than tree growth, so once a seedling has established, a tree will be able to grow. However, this growth is possible only if there is sufficient shade of neighbors. So in our model, growth inhibition and mortality are lowered by the presence of neighbors. In the Wiegand et al. (2006) model, the reason for the low growth inhibition and rapidly dropping mortality with age are not specified, but are in fact positive feedbacks between tree age and survival.

Increasing shade and decreasing radiation tolerance are two ways of increasing the relative advantage of being shaded. This relative advantage is also greater under high external radiation, which indeed caused a lowering of the treeline in our model (not shown). Consequently, slopes that receive high solar radiation can be expected to have treelines at lower altitudes compared to slopes that receive less radiation. Especially, slopes that receive radiation in the early morning, when plants are still cold from the preceding night and therefore more susceptible to cold-induced photoinhibition, can be expected to have low treelines. This pattern is indeed found at treelines in central Ecuador (Bader and Ruijten, 2008).

The inhibiting effect of shade dependence and fire on treeline advance may explain why many tropical alpine treelines are located at altitudes below what may be the temperature limit for trees. Many treelines may not have kept up with the climatic warming since the late glacial. In fact, such slow advance during the Holocene is evident from paleoecological field data from a treeline in northern Ecuador (Di Pasquale et al., 2008), although paleoecological data from other tropical treelines may indicate faster treeline fluctuations (Van Der Hammen, 1974; Flenley, 1979; Wille et al., 2002).

Most tropical treelines are very abrupt boundaries (Bader et al., 2007a). Fire is usually a common phenomenon in the alpine vegetation, and as shown by our model it may explain the abruptness of these treelines as well as their apparent stability. This is in accordance with the dominant explanation for the abruptness of treelines in tropical mountains (Laegaard, 1992; Miehe and Miehe, 1994). However, we have shown that this abruptness and stability can also be explained by shade dependence of treeline forest trees. An abrupt treeline does therefore not necessarily indicate that it is shaped by fire, but may indicate that the tree species in the treeline forest are shade dependent. The abruptness of a treeline can also indicate the type of response that can be expected after climatic warming (Armand, 1985, 1992). Treelines may then be naturally inclined to shift, but shade dependence of the trees would strongly slow down such a shift, as would fire in the páramo. At treelines where fire plays an important role, a cessation of páramo burning would have a far greater effect on treeline patterns and dynamics than a rise in temperature.

Acknowledgments

We thank Felix Herzog, Pita Verweij, and Frank van Langevelde for their helpful comments on the manuscript. The research of Rietkerk is supported by a VIDI grant from the Netherlands Organization for Scientific Research, division Earth and Life Sciences (NWO-ALW).

References Cited

Alftine, K. J., and Malanson, G. P., 2004: Directional positive feedback and pattern at an alpine tree line. *Journal of Vegetation Science*, 15: 3–12.

Armand, A. D., 1985: The change of vegetation near the timberline. *Inter-Nord*, 17: 59–62.

Armand, A. D., 1992: Sharp and gradual mountain timberlines as a result of species interaction. *In* Hansen, A. J., and Castri, F. d. (eds.), *Landscape boundaries: consequences for biotic diversity and ecological flows*. New York: Springer.

Bader, M. Y., and Ruijten, J., 2008: A topography-based model of forest distribution at alpine treeline in the tropical Andes. *Journal of Biogeography*, 35: 711–723.

Bader, M. Y., Rietkerk, M., and Bregt, A. K., 2007a: Vegetation structure and temperature regimes of tropical alpine treelines. *Arctic, Antarctic, and Alpine Research*, 39: 353–364.

Bader, M. Y., van Geloof, I., and Rietkerk, M., 2007b: High solar radiation hinders tree establishment above the alpine treeline in northern Ecuador. *Plant Ecology*, 191: 33–45.

Ball, M. C., Hodges, V. S., and Laughlin, G. P., 1991: Cold-induced photoinhibition limits regeneration of snow gum at tree-line. *Functional Ecology*, 5: 663–668.

Barber, J., and Andersson, B., 1992: Too much of a good thing: light can be bad for photosynthesis. *Trends in Biochemical Sciences*, 17: 61–66.

Bruno, J. F., Stachowicz, J. J., and Bertness, M. D., 2003: Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, 18: 125.

Caldwell, M. M., Robberecht, R., and Billings, W. D., 1980: A steep latitudinal gradient of solar ultraviolet-B radiation in the arctic-alpine life zone. *Ecology*, 61: 600–611.

Camarero, J. J., Gutiérrez, E., and Fortin, M. J., 2000: Spatial pattern of subalpine forest–alpine grassland ecotones in the Spanish Central Pyrenees. *Forest Ecology and Management*, 134: 1–16.

Close, D. C., Beadle, C. L., Brown, P. H., and Holz, G. K., 2000: Cold-induced photoinhibition affects establishment of *Eucalyptus nitens* (Deane and Maiden) Maiden and *Eucalyptus globulus* Labill. *Trees—Structure and Function*, 18: 32–41.

Di Pasquale, G., Marziano, M., Impagliazzo, S., De Natale, A., Lubritto, C., and Bader, M. Y., 2008: The Holocene treeline in the northern Andes (Ecuador): first evidence from soil charcoal. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 259: 17–34.

Dullinger, S., Dirnböck, T., and Grabherr, G., 2004: Modelling climate change–driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology*, 92: 241–252.

Falowski, P. G., Greene, R., and Kolber, Z., 1994: Light utilization and photoinhibition of photosynthesis in marine phytoplankton. *In* Baker, N. R., and Bowyer, J. R. (eds.), *Photoinhibition of photosynthesis—From molecular mechanisms to the field*. Oxford: BIOS Scientific Publishers, 407–432.

Flenley, J. R., 1979: The Late Quaternary vegetational history of the equatorial mountains. *Progress in Physical Geography*, 3: 488–509.

Germino, M. J., and Smith, W. K., 1999: Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant, Cell and Environment*, 22: 407–415.

Graumlich, L. J., Waggoner, L. A., and Bunn, A. G., 2004: Detecting global change at alpine treeline: coupling paleoecology with contemporary studies. *In* Huber, U., Bugmann, H., and Reasoner, M. (eds.), *Global change and mountain regions: a state of knowledge overview*. Dordrecht: Springer, 405–412.

Hofstede, R., Segarra, P., and Mena Vásconez, P., 2003: *Los páramos del Mundo*. Quito: Proyecto Atlas Mundial de los Páramos. Global Peatland Initiative/NC-IUCN/EcoCiencia.

Hofstede, R. G. M., Mondragon Castillo, M. X., and Rocha Osorio, C. M., 1995: Biomass of grazed, burned, and undisturbed páramo grasslands, Colombia. I. Aboveground vegetation. *Arctic and Alpine Research*, 27: 1–12.

Holtmeier, F. K., and Broll, G., 2005: Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, 14: 395–410.

Huisman, J., 1997: The struggle for light. Ph.D. thesis. Rijksuniversiteit Groningen: Groningen, Netherlands.

Huner, N. P. A., Öquist, G., and Sarhan, F., 1998: Energy balance and acclimation to light and cold. *Trends in Plant Science*, 3: 224–230.

IPCC, 2007: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L. (eds.). Cambridge: Cambridge University Press, 996 pp.

Körner, C., 1998: Worldwide position of alpine treelines and their causes. *In* Beniston, M., and Innes, J. L. (eds.), *The impacts of climate variability on forests*. Berlin, New York: Springer, 221–229.

Krause, G. H., 1994: Photoinhibition induced by low temperatures. *In* Baker, N. R., and Bowyer, J. R. (eds.), *Photoinhibition of photosynthesis—From molecular mechanisms to the field*. Oxford: BIOS Scientific Publishers, 331–348.

Kupfer, J. A., and Cairns, D. M., 1996: The suitability of montane ecotones as indicators of global climatic change. *Progress in Physical Geography*, 20: 253–272.

Laegaard, S., 1992: Influence of fire in the grass páramo vegetation of Ecuador. *In* Balslev, H., and Luteyn, J. L. (eds.), *Páramo. An Andean ecosystem under human influence*. London: Academic Press, 151–170.

Landsberg, J. J., 1986: *Physical ecology of forest production*. London: Academic Press, 198 pp.

Long, S. P., Humphries, S., and Falkowski, P. G., 1994: Photoinhibition of photosynthesis in nature. *Annual Review of Plant Physiology and Plant Molecular Biology*, 1994: 633–662.

Malanson, G. P., 1997: Effects of feedbacks and seed rain on ecotone patterns. *Landscape Ecology*, 12: 27–38.

Malanson, G. P., 2001: Complex responses to global change at alpine treeline. *Physical Geography*, 22: 333–342.

Miehe, G., and Miehe, S., 1994: Zur oberen Waldgrenze in tropischen Gebirge. *Phytocoenologia*, 24: 53–110.

Noble, I. R., 1993: A model of the responses of ecotones to climate change. *Ecological Applications*, 3: 396–403.

Resler, L. M., 2006: Geomorphic controls of spatial pattern and process at alpine treeline. *Professional Geographer*, 58: 124–138.

Rietkerk, M., and van de Koppel, J., 1997: Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos*, 79: 69–76.

Rietkerk, M., Boerlijst, M. C., van Langevelde, F., Hille Ris Lambers, R., van de Koppel, J., Kumar, L., Prins, H. H. T., and de Roos, A. M., 2002: Self-organization of vegetation in arid ecosystems. *American Naturalist*, 160: 524–530.

Rietkerk, M., Dekker, S. C., de Ruiter, P. C., and van de Koppel, J., 2004: Self-organized patchiness and catastrophic shifts in ecosystems. *Science*, 305: 1926–1929.

Rundel, P. W., 1994: Tropical alpine climates. *In* Rundel, P. W., Smith, A. P., and Meinzer, F. C. (eds.), *Tropical alpine environments. Plant form and function*. Cambridge: Cambridge University Press, 21–44.

Sarmiento, G., 1986: Ecological features of climate in high tropical mountains. *In* Vuilleumier, F., and Monasterio, M. (eds.), *High altitude tropical biogeography*. New York, Oxford: Oxford University Press, 11–45.

Scheffer, M., and Carpenter, S. R., 2003: Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution*, 18: 648–656.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., and Walker, B., 2001: Catastrophic shifts in ecosystems. *Nature*, 413: 591–596.

Slayter, R. O., and Noble, I. R., 1992: Dynamics of montane treelines. *In* Hansen, A. J., and di Castri, F. (eds.), *Landscape boundaries: consequences for biotic diversity and ecological flows*. New York: Springer, 346–359.

Smith, W. K., Germino, M. J., Hancock, T. E., and Johnson, D. M., 2003: Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23: 1101–1112.

Spitters, C. J. T., 1986: Separating the diffuse and direct component of global radiation and its implications for modelling canopy photosynthesis. Part II. Calculation of canopy photosynthesis. *Agricultural & Forest Meteorology*, 38: 231–242.

Stainforth, D. A., Aina, T., Christensen, C., Collins, M., Faull, N., Frame, D. J., Kettleborough, J. A., Knight, S., Martin, A., Murphy, J. M., Piani, C., Sexton, D., Smith, L. A., Splcer, R. A., Thorpe, A. J., and Allen, M. R., 2005: Uncertainty in predictions of the climate response to rising levels of greenhouse gases. *Nature*, 433: 403–406.

Suarez, R. E., and Medina, G., 2001: Vegetation structure and soil properties in Ecuadorian páramo grasslands with different histories of burning and grazing. *Arctic, Antarctic, and Alpine Research*, 33: 158–164.

Van Der Hammen, T., 1974: The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography*, 1: 3–26.

Wardle, P., 1965: A comparison of alpine timber lines in New Zealand and North America. *New Zealand Journal of Botany*, 3: 113–135.

Wardle, P., 1985: New Zealand timberlines. 1. Growth and survival of native and introduced tree species in the Craigieburn Range, Canterbury. *New Zealand Journal of Botany*, 23: 219–234.

Wiegand, T., Camarero, J. J., Rüger, N., and Gutiérrez, E., 2006: Abrupt population changes in treeline ecotones along smooth gradients. *Journal of Ecology*, 94: 880–892.

Wille, M., Hooghiemstra, H., Hofstede, R., Fehse, J., and Sevink, J., 2002: Upper forest line reconstruction in a deforested area in northern Ecuador based on pollen and vegetation analysis. *Journal of Tropical Ecology*, 18: 409–440.

Wilson, J. B., and Agnew, A. D. Q., 1992: Positive-feedback switches in plant communities. *Advances in Ecological Research*, 23: 263–336.

Ms accepted June 2007