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FIFTEEN YEARS OF REVEGETATION OF MOUNT ST. HELENS: A LANDSCAPE-SCALE ANALYSIS

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Abstract. Understanding vegetation responses to landscape-scale disturbance often is critical for understanding ecosystem structure and function. Satellite remote sensing and geographic information systems can be used to determine whether response patterns observed in fine-scale studies are present at landscape scales. We used these technologies to examine key factors correlated with revegetation of Mount St. Helens in the first 15 yr following its catastrophic eruption in 1980. To measure revegetation, we used eight Landsat satellite scenes from 1984 to 1995 to estimate for each pixel (1) the time (in years) to reach an estimated 10% vegetation cover (EC10), (2) maximum rate of increase in vegetation cover (MR), (3) time-integrated vegetation cover (TIC), and (4) maximum estimated cover reached during the study period (MEC). Explanatory variables included type of volcanic disturbance, distance from the eruption, initial tephra thickness, distance from surviving forests, and topographic variables. Regression tree analysis (RTA) was used to model the response variables with the explanatory variables.

RTA explained 50% of the variation in EC10, 57% of the variation in TIC, 31% of the variation in MR, and 51% of the variability in MEC. Remaining variability was a function of other variables, stochastic factors, and image processing. The greatest amount of variability in revegetation was explained by type of volcanic disturbance, which stratified the study area into primary and secondary successional areas and revealed previously undocumented patterns of where each successional type was present.

Under secondary successional conditions, distance from the eruption and original tephra thickness were important. For primary successional areas, proximity to forest edges was important only at the edges of mudflows. Slope gradient was important for both secondary and primary successional areas. Landscape-scale patterns of revegetation were consistent with field studies of the importance of biotic legacies, colonizing vegetation, and topography. However, the importance of slope gradient for revegetation in primary successional areas has not been previously reported.

Key words: *disturbance; geographic information systems; landscapes; Mount St. Helens, Washington; regression tree analysis; remote sensing; revegetation; volcanoes.*

INTRODUCTION

Disturbance plays a critical role in shaping vegetation communities (White 1979). Infrequent landscape-scale disturbances affect such critical characteristics as species composition, ecosystem productivity, and nutrient distribution (Vance and Wilson 1990). In the Pacific Northwest United States, both wildfire and volcanic activity at scales from several hectares to several hundred thousand hectares have determined vegetation structure at time scales well within the life span of dominant tree species (Franklin et al. 1988). Thus, understanding vegetation response to landscape-scale disturbance is vital to understanding ecosystem structure and function.

Despite the importance of landscape-scale disturbance, most studies of vegetation responses have been conducted at finer scales for two primary reasons. First, most processes affecting vegetation response occur at fine scales and, therefore, fine-scale studies of patterns allow stronger inferences about the processes. Second, the tools for examining landscape-scale patterns, including remote sensing and geographic information systems (GIS), are relatively new, and analytical techniques for linking observed vegetation patterns to response processes are less developed.

Unfortunately, differences in scale between the patterns observed and the processes weaken inferences (Levin 1992), and conclusions from fine-scale studies are not automatically valid at landscape or management-level scales (Wiens 1989). In this study, we tested, at landscape scales, conclusions based on fine-scale studies. Based on previous studies, we (1) developed hypotheses regarding landscape-scale patterns that could be observed using remotely sensed data; (2) determined whether observed landscape-scale patterns

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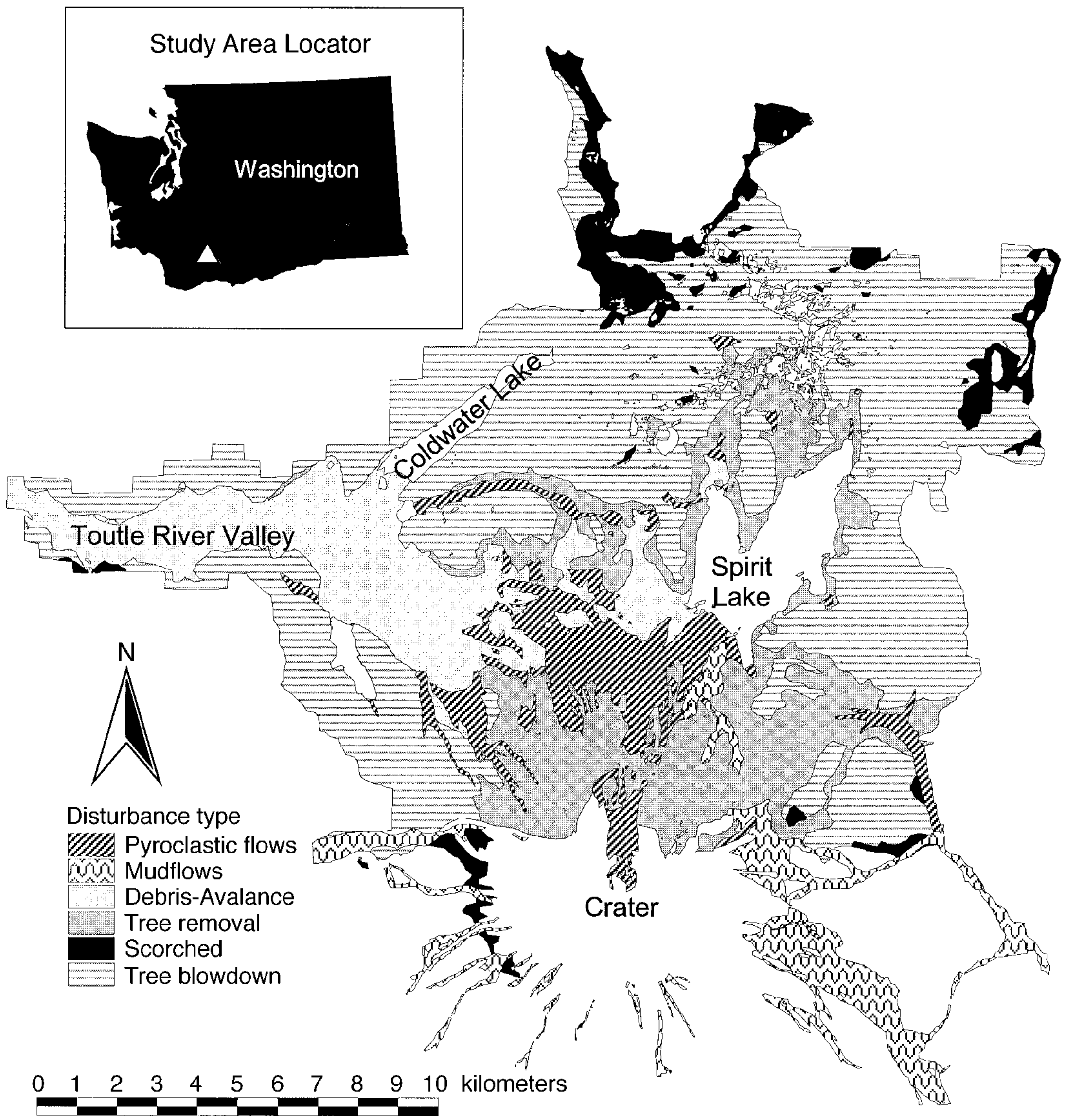

FIG. 1. Study area map, showing major types of volcanic disturbance resulting from the 1980 eruptions of Mount St. Helens. See Table 2 for a more detailed description of the disturbance types and subcategories. The map is based on Lipman and Mullineaux (1981).

were consistent with our hypotheses using nonexperimental, analytical methods (Eberhardt and Thomas 1991); (3) examined the test results to determine whether conclusions about vegetation responses could be reached by induction; and (4) identified further lines of inquiry at fine scales based on our results. This approach both avoided the pitfalls of using landscape-scale data to study fine-scale processes and let us apply fine-scale studies at management-relevant scales.

Biotic legacies, including surviving seeds and roots (survivors), accessible organic soils, and organic debris, most notably downed trees, persisted over large portions of the devastated area after the Mount St. Helens eruptions. Early studies of post-eruption vegetation showed dominance by surviving individuals (Franklin et al. 1985), in some cases as a result of protection by a heavy, but patchy spring snowpack (Halpern et al. 1990, Frenzen 1992). More often, however, specific biotic legacies are correlated with the complex mosaic of volcanic deposits (Means et al. 1982, del Moral and Bliss 1993) (Fig. 1). Survivors are often associated with the presence of coarse organic debris and accessible organic soils under thin volcanic deposits (Halpern et al. 1990). These factors can assist in revegetation, with organic soils providing nitrogen absent from juvenile volcanic materials and organic debris providing beneficial microsites for seedling establishment (Frenzen and Franklin 1985, Halpern et al. 1990). While biotic legacies are critical to understanding revegetation patterns, legacies cannot be measured directly with remote sensing. We used disturbance patterns as a proxy because disturbances determined presence and abundance of biotic legacies. We hypothesized that: Revegetation at Mount St. Helens was more rapid (1) where disturbance mechanisms allowed the presence of biotic legacies and (2) in the likely presence of biotic legacies, where disturbances were less intense resulting in the likely greater abundance of biotic legacies.

Where biotic legacies were unlikely, initial revegetation depended on colonizing seeds. Few fine-scale studies have shed light on patterns of revegetation across these areas. Plot-based studies suggest that rates of revegetation in primary successional areas are higher near pools of survivors (del Moral and Bliss 1993). At Mount St. Helens, relatively undisturbed areas surrounding the devastated area were predominantly forested, and a relationship has been found between revegetation and distance from forested edges (Halpern and Harmon 1983). We therefore hypothesized that: (3) Initial revegetation for areas unlikely to have biotic legacies would be positively correlated with proximity to forested edges. However, remotely sensed data could not determine the source of subsequent revegetation (colonizing vegetation or expansion of vegetation from within the devastated area).

In addition to volcanic disturbance mechanisms, subsequent geomorphic processes might further alter the landscape in ways that could affect revegetation. For instance, depth of burial is critical to buried-vegetation response (Zobel and Antos 1997), and erosion on steeper slopes might uncover survivors and assist revegetation (del Moral 1983), while accumulations on flat areas and in depressions might inhibit revegetation. This process would not affect revegetation where survivors were not present. Therefore, we hypothesized that: (4) Revegetation for areas that were likely to have survivors would be more rapid on steeper slopes.

Other topographic variables can also affect revegetation (Sharpe et al. 1995). Increasing elevation is related to decreases in temperature and evapotranspiration and increases in precipitation and snow depth (Allen and Peet 1990). Topographic aspect combines with slope steepness to affect solar exposure, available radiation, and evapotranspiration. However, studies of these topographic variables at Mount St. Helens have not revealed strong correlations with revegetation (Halpern et al. 1990). Therefore, we hypothesized that: Revegetation would not be correlated with (5) elevation or (6) aspect.

We have previously reported landscape-scale patterns of revegetation and temporal changes in these patterns for the first 15 yr after the eruption (Lawrence and Ripple 1998, 1999). Here we report our findings of how these spatial and temporal patterns related to findings from an extensive history of fine-scale research at Mount St. Helens.

Methods

We used satellite images, a GIS, and statistical analyses to examine the relative importance of potential influences on landscape-scale revegetation of Mount St. Helens. Satellite imagery was used to characterize patterns of revegetation for the period 1980 to 1995. GIS layers were constructed to provide the explanatory data for our statistical analyses.

Study area

For this study, we examined 25 400 ha of the area devastated by the 1980 eruptions of Mount St. Helens that have been allowed to recover with a minimum of human intervention (Fig. 1). As of 1995, vegetation in this area was highly variable in amount, ranging from 0% to 100% cover, and type, including grass-, forb-, and shrub-dominated communities, as well as conifer and hardwood trees. A detailed description of the study area is in Lawrence and Ripple (1998).

Variables

Conceptually, our response variable was revegetation of the Mount St. Helens devastated area. Although revegetation can be characterized by the change in vegetation amount between two dates, this approach would not differentiate among processes that might result in identical beginning and ending values but follow very different paths of growth. Therefore, we used eight dates of Landsat Thematic Mapper (TM) images to estimate, for each 25×25-m pixel in the images, change curves representing the trajectories for estimated green vegetation cover (estimated cover) within each pixel (Lawrence and Ripple 1999). From these change curves, we extracted several measures of change (e.g., maximum estimated cover) in green vegetation cover for each of $\sim$400 000 pixels within the satellite images.

We selected response variables to compare early vegetation recovery with responses over the longer term and overall responses. To measure early vegetation responses, we used the change curves to calculate the number of years necessary to reach 10% estimated cover (EC10). We selected the 10% level because it was the minimum level used to calculate estimated cover. We selected the maximum estimated cover (MEC) during the study period, the greatest value for each change curve, as our late response variable. To characterize overall vegetation response, we used (1) the total area under the change curve, or time-integrated estimated cover during the study period (TIC), and (2) the maximum rate of increase in the change curve, or maximum first derivative (MR).

Explanatory variables (Table 1) were input to a GIS, geo-referenced, and converted to raster format with 25-m pixels to match our response layers. Hypothesis 1 relating to disturbance mechanisms was analyzed using a disturbance-type layer, which reflected differences in

TABLE 1. GIS layers used for explanatory variables in a study of the revegetation of Mount St. Helens after its 1980 eruption.

GIS layer/variable	Range of values	Original data source
Disturbance type	(see Table 2)	Lipman and Mullineaux (1981)
Distance from crater	0–21.3 km	30-m DEM and Lipman and Mullineaux (1981)†
Tephra thickness	2–200 cm	Waitt et al. (1981)
Blast exposure	directly exposed and unexposed	30-m DEM and Voight (1981)
Distance from surviving forests	25–8225 m	Lipman and Mullineaux (1981)
Slope gradient	0–68 degrees	30-m DEM
Slope curvature	degree of convexity or concavity	30-m DEM
Elevation	476–2493 m	30-m DEM
Aspect	N, S, E, W, and flat	30-m DEM

† DEM = digital elevation model.

amount of burial, temperature, and force (Table 2) and, therefore, likelihood of presence of biotic legacies. For Hypothesis 2, regarding intensity of disturbances, distance from the crater was examined because each disturbance type was probably less intense in thickness, temperature, and force with distance from the eruption. In addition, tephra thickness affected intensity of burial and topographic protection from the lateral blast potentially reduced the heat and force of the blast. Distance from surviving forests was measured directly for Hypothesis 3. To analyze erosion on steeper slopes for Hypothesis 4, we computed slope gradient and curvature. Elevation and aspect were computed to test Hypotheses 5 and 6.

Statistical analysis

We used regression tree analysis (RTA) to model our four response variables using the nine explanatory variables. RTA is a computationally intensive approach that analyzes all explanatory variables and determines which binary division of a single explanatory variable best reduces deviance (defined as squared residuals) in the response variable (Breiman et al. 1984, Efron and Tibshirani 1991). For each portion of the data resulting from this first split, the process is repeated, continuing until homogeneous ending points (terminal nodes) are reached in a hierarchical tree. A common alternative, multiple linear regression, applies explanatory variables continuously, rather than by binary splits, does not readily handle nonlinear relations, and has difficulty modeling complex interactions, especially among continuous and categorical explanatory variables.

With a complex set of explanatory variables, the appropriate technique can be difficult to determine. Because both multiple linear regression and RTA are based on minimizing squared residual deviance, the amount of variation explained by these two models can be directly compared. We compared our RTA models with our best multiple linear regression fits using an independent validation data set of 1000 points. In all cases, RTA explained substantially more variability in the response variable than did multiple linear regression. Therefore, we used RTA for our analysis, as implemented in the S-Plus statistical package (Venables and Ripley 1994, MathSoft 1995). For each of 5000 random points, we extracted all four response and all

TABLE 2. Types and intensity of disturbances resulting from the 1980 eruption of Mount St. Helens, based on classification by U.S. Geological Survey (Lipman and Mullineaux 1981).

Type	Thickness (m)	Temperature (°C)	Speed (m/s)
Pumiceous pyroclastic flow deposits			
16–18 Oct, 7 Aug, 22 July, 12 June, 25 May, 18 May deposits	≤40	300–700	≤28
Mudflow features			
Deposits	≤4	<100	1–31
Scour areas	0	<100	1–31
Features of the directed blast			
Pyroclastic flow	≤10	70–277	28–167
Deposit above treeline, scorched, tree blowdown, and tree removal zones	≤1	100–350	28–167
Debris-avalanche deposits			
Mudflow, North Toutle, Spirit Lake, Coldwater Ridge, and Marginal units	20–195	68–98	39–61

nine explanatory variables. These data were transferred to an S-Plus data frame and regression trees were fit for each response variable.

RTA generally will overfit the model, so that the tree must be pruned. To prune the regression trees, we used a cross validation method (Venables and Ripley 1994), randomly dividing the data into ten equal sets of 500 points each. Trees were generated for nine of the data sets and validated against the tenth, with the lowest mean square error for the validation indicating the best size tree (increasing mean square error with increasing tree size indicates that the tree is overfit). Because different random divisions can produce different size trees, we ran the cross validation procedure ten times and selected as the best tree size the smallest tree within one standard error of the mean of the ten runs.

To further test the quality of the final regression trees, we validated the trees against an independent data set. We extracted response and explanatory variable data for a second random set of 5000 points. For this validation data, predicted values were produced from each final regression tree. These predicted values were used to calculate residual errors and coefficients of determination (R^2) for comparison with the original data used to produce the trees. The final validated regression trees were used to prepare, for each explanatory variable, a response surface of predicted values to analyze visually the results of the regression trees.

Results

Regression trees for EC10, TIC, and MEC (Fig. 2) explained 50–57% of the variability in our original data and 46–54% in the validation data (Table 3). The regression tree for MR, which was designed to measure overall responses like TIC, is excluded from the remainder of the *Results* and *Discussion* because it produced a regression tree essentially identical to TIC, but explained 26% less variability than TIC. Variables included differed for each regression tree, although disturbance type, distance from crater, distance from surviving forests, and slope gradient were included in all regression trees (Table 3). Response surfaces showing predicted values across the study area demonstrated that patterns of revegetation varied substantially depending on the response variable (Fig. 3).

The regression trees can be used to determine the importance of each explanatory variable relative to each response variable, the conditions under which each explanatory variable is important, the predicted value for each path through the regression trees, and the total land area for each predicted value. The response surfaces show the spatial location for each path through the regression tree. For example, in the regression tree for EC10 (Fig. 2), for tree blowdown, scorched, mudflow scour, and debris-avalanche marginal areas <11 km from the crater and at slope gradients <15.5°, the predicted value is 19 yr to reach 10% cover and 1791 ha fit these conditions (mapped in light green on the EC10 map in Fig. 3).

We were not able to reject any of our hypotheses except Hypothesis 5 relating to elevation and Hypothesis 6 relating to aspect. The results, however, did indicate differences in the relative importance of hypothesized influences on revegetation. Volcanic disturbance mechanisms (Hypothesis 1) were the most important. For all four regression trees, the first tree division was based on disturbance types, effectively stratifying the study area into (1) secondary successional areas where substantial survivors (as well as other biotic legacies such as down trees) might be present or organic soils were thinly overlaid with volcanic deposits and (2) primary successional areas where most biota and organic soils were either deeply buried, removed by erosion, or seared by heat. Observations from the tree blowdown zone, the scorched zone, the mudflow scour area, and the debris-avalanche marginal unit showed that they averaged faster or greater revegetation in each regression tree. Although the tree blowdown and scorched zones have been noted in previous studies as areas of secondary succession (e.g., Means et al. 1982), the debris-avalanche marginal unit consisted primarily of stream valley floor alluvium, which was rich in organic soils and debris, while the mudflow scour areas were not subject to the thick residual deposits of the primary mudflows (Lipman and Mullineaux 1981). Therefore, these areas were collectively distinguishable because secondary succession was taking place and other biotic legacies might be present. Disturbance types that were not included in this group included all pyroclastic flows, the main portions of the mudflows, the main portions of the debris-avalanche, and the tree removal zone. Pyroclastic flows and most of the mudflows and debris avalanche were covered with thick deposits of juvenile soils and had minimal surviving plants or sproutable plant parts (del Moral 1983, del Moral and Bliss 1993). The tree removal zone was an area of erosion caused by the lateral blast, which removed essentially all organic material (Lipman and Mullineaux 1981).

Variables related to disturbance intensity in secondary successional areas (Hypothesis 2) were included in all regression trees. In these areas, distance from crater was important for 13 725 ha for early vegetation response (EC10), but only 1549 ha for TIC and 7775 ha for MEC. Airfall tephra thickness was important only for overall (TIC) and late (MEC) measures of vegetation response. Exposure to direct impact of the lateral blast was generally not important except for 3016 ha of the MEC regression tree.

Distance from forested edges (Hypothesis 3) was important for all of the regression trees in primary successional areas, including 5113 ha for EC10, 10 931 ha for TIC, and 10 686 ha for MEC. The impact of this variable was located primarily at the edges of mudflows.

The importance of slope steepness (Hypothesis 4) was strongly supported, although the associated vari-

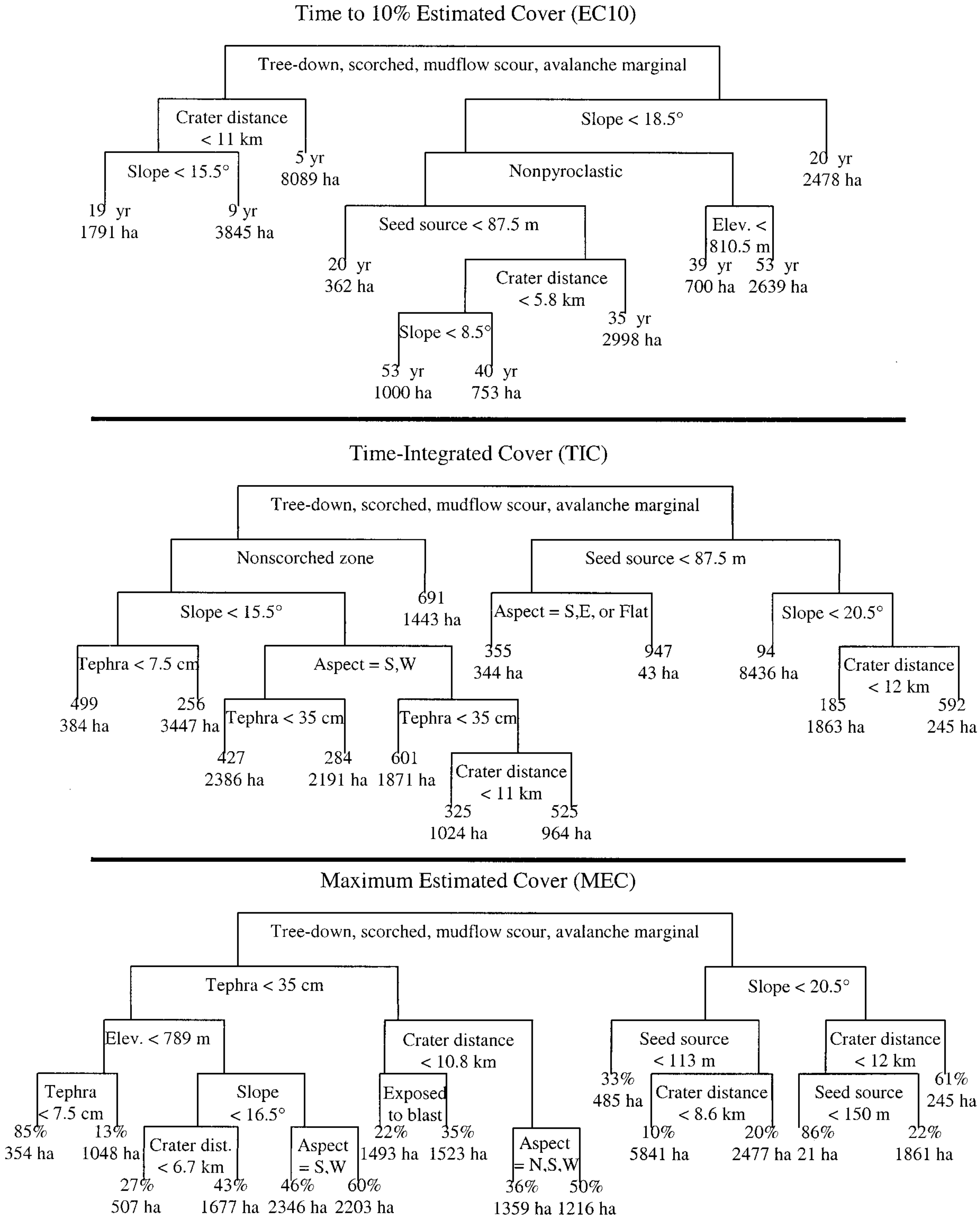

FIG. 2. Final regression trees for EC10, TIC, and MEC. Text at splits in each regression tree indicates conditions for the left branchings in the tree. Numbers at terminal nodes are for observations meeting the conditions leading through the tree: top numbers are estimated response values, and bottom numbers are areas meeting such conditions. Note that TIC values are unitless.

TABLE 3. The amount of variability explained by, and variables included in, each regression tree for 5000 points used to model the regression trees and an independent set of 5000 points.

Regression-tree characteristic	Regression tree			
	EC10	TIC	MR	MEC
R^2	0.50	0.57	0.37	0.51
Validation R^2	0.46	0.54	0.31	0.47
Included variables				
Disturbance type	√	√	√	√
Distance from crater	√	√	√	√
Tephra thickness		√	√	√
Blast exposure			√	√
Distance from surviving forests	√	√	√	√
Slope gradient	√	√	√	√
Slope curvature				
Elevation	√			√
Aspect		√	√	√

able of slope curvature was not included in any regression tree. Areas where slope gradient was not important included (1) for EC10, primary successional areas ≥11 km from the crater, (2) for TIC, areas at the edges of mudflows and tree scorched areas, and (3) for MEC, secondary successional areas with airfall tephra ≥35 cm and, for areas with thinner airfall tephra layers, areas >789 m in elevation. Although the broad importance of slope gradient was consistent with Hypothesis 4, the inclusion of slope gradient as an important factor in primary successional areas was unexpected.

Although we were not able to conclusively reject Hypotheses 5 and 6 regarding elevation and aspect, they had little importance in the regression trees. Elevation was important only for 3339 ha in EC10 and 8135 ha in MEC. Similarly, aspect was a factor only at the edges of mudflows and on limited steep slopes for TIC and in very limited areas for MEC.

DISCUSSION

A substantial portion of the variation in vegetation response was explained by variables supporting Hypotheses 1–4. The relative amount of variation related to volcanic disturbance mechanisms and intensity, distance from forest edges, and slope gradient, however, indicated that the importance of these influences on revegetation was not equal.

After 15 yr of revegetation, disturbance types remained the most influential factor we tested (Fig. 4). The initial stratification of the data for all response variables is best explained by the effect of disturbance mechanisms on pre-eruption biota. Faster revegetation was consistently observed in the tree blowdown, scorched, mudflow scour, and debris-avalanche marginal areas, which contained substantial biotic legacies. This pattern corresponds to expected differences in primary vs. secondary successional processes (e.g., Vitousek and Walker 1987). Our findings are consistent with previous studies at Mount St. Helens finding slow revegetation in pyroclastic, mudflow, and debris avalanche zones (del Moral and Bliss 1993) and documenting early soil building processes (Ugolini et al. 1991), as well as early, rapid revegetation in areas where survivors were present (Franklin et al. 1988).

Dominance by biotic legacies in early revegetation means that vegetation responses to volcanic disturbance might not follow predictable successional patterns absent knowledge of surviving species and their spatial distribution. Although deterministic successional stages for succession following volcanic disturbance have been postulated (Eggler 1963, Smathers and Mueller-Dombois 1974) based on concepts of facilitation (Clements 1916) and relay floristics, other studies in disturbance ecology have noted the importance of initial floristics (e.g., Egler 1954, Connell and Slatyer 1977, Vitousek and Walker 1987, Halpern and Franklin 1990) and other biological legacies (Franklin et al. 1985). Our findings were consistent with these latter studies.

The pace of primary succession is slow relative to secondary succession, however opportunities to quantify the difference without substantial confounding factors are rare. The presence of primary and secondary succession side by side at Mount St. Helens allowed us to make such a comparison while controlling for many factors. The average time to reach EC10 in primary successional areas was 38 yr, compared to eight years for secondary successional areas, almost five times as long. Average MEC during the study period for primary successional areas was 16%, compared to 44% for other areas, and TIC in primary successional areas averaged one-third of that in secondary successional areas.

Consistent with Hypothesis 2, tephra thickness was not important in primary successional areas where tephra covered other, juvenile material, but was important in secondary successional areas for overall and long-term responses. Survival and recovery of vegetation under tephra layers has been previously documented at Mount St. Helens (Zobel and Antos 1997) and other volcanoes (e.g., Griggs 1918, Taylor 1957). In each case, vegetation response was dependent on the

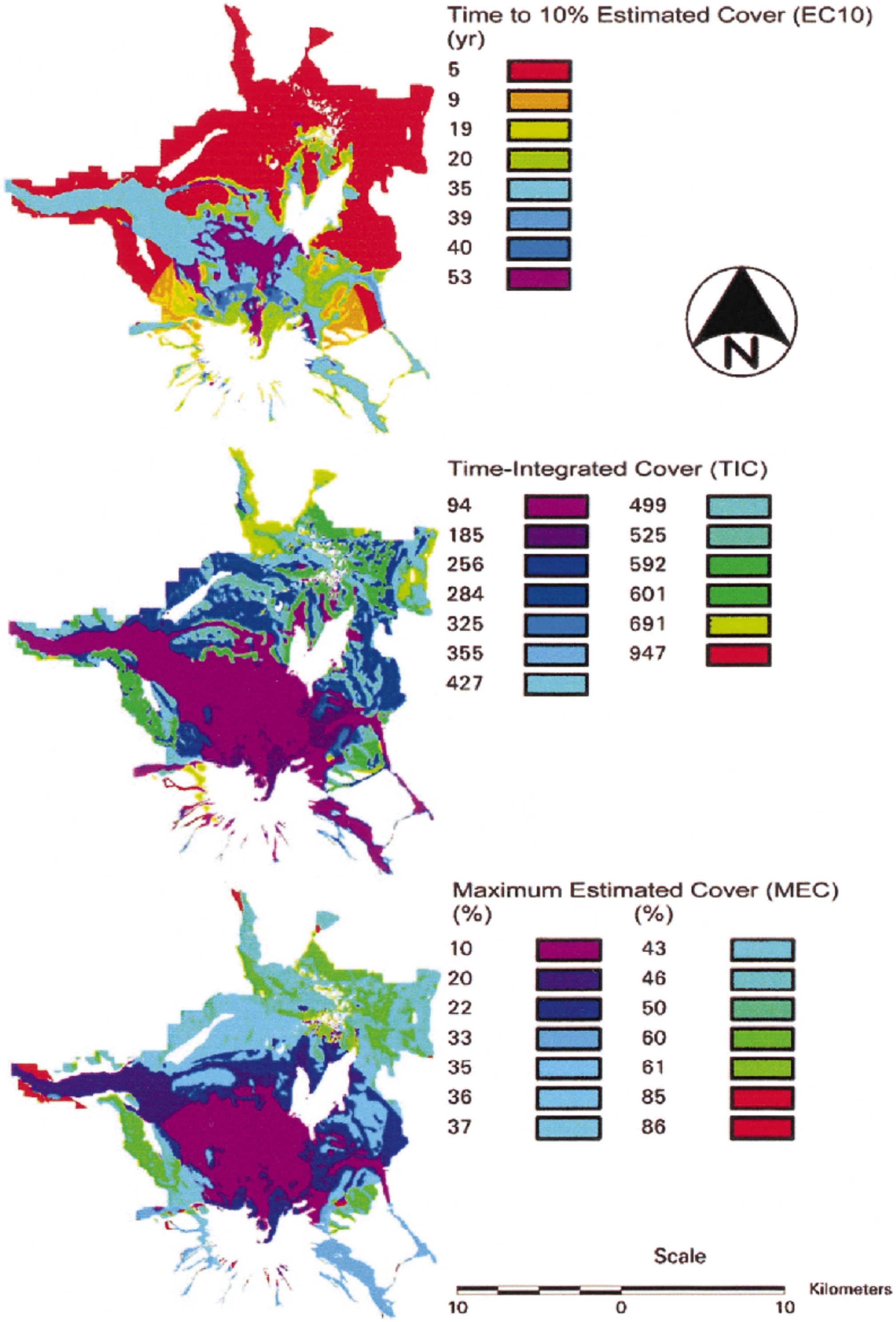

FIG. 3. Response surfaces based on regression trees for EC10, TIC, and MEC. Note that TIC values are unitless.

thickness of the tephra layers and species' abilities to penetrate covering layers.

The importance of distance from the crater was also consistent with Hypothesis 2. The importance of distance from the crater, even within disturbance types, reflects a reduction in the heat and force of the lateral blast with distance, which likely resulted in greater abundance of survivors at greater distances.

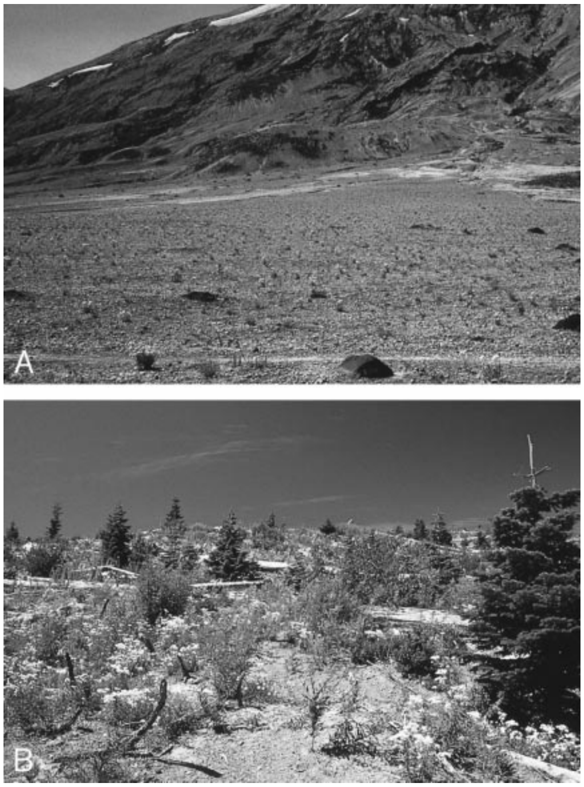

FIG. 4. Comparison of typical landscapes in 1996 for (A) a primary successional area (Plains of Abraham) and (B) a secondary successional area (Independence Pass).

Hypothesis 3, regarding proximity to forest edges, was not strongly supported by our analysis, although we were not able to completely reject the hypothesis. In primary successional areas, sites within 87–150 m of surviving forests had greater revegetation for all response variables. (These conditions existed only on mudflows to the east and south of the crater.) Our finding on forest edge proximity is consistent with early studies of the Muddy River mudflow to the east of the crater (Halpern and Harmon 1983) and the Kautz Creek mudflow on nearby Mount Rainier (Frenzen et al. 1988). At each location, seedling densities dropped significantly in plots >100–150 m from forested edges. This finding is explained by a predominance of heavy, poorly dispersing seeds from the adjoining forests (Wood and del Moral 1987). (This pattern might be confounded by the dynamics of the mudflows, which had less force and thinner deposits toward their edges.) The absence of distinctions at greater distances indicated that distance from forests was probably not an important factor for light, wind-blown seeds, which were the primary colonizers on primary successional sites at Mount St. Helens (del Moral and Bliss 1993). The lack of success of these species in these harsh sites has been documented (Wood and del Moral 1987) and related to the trade-offs between colonizing ability and stress tolerance (Grime 1979).

In secondary successional areas, distance from forest edges was generally not important because of the dominance of survivors. In general, colonizing vegetation has not been as important a factor in revegetation as survivors when survivors are present (e.g., Griggs 1918, Eggler 1963). Where distance from forest edges was important within secondary successional area (in the scorched zone within ~400 m of forest edges for TIC), greater amounts of upright, dead vegetation might have captured wind-blown seeds and resulted in enhanced revegetation.

While patterns consistent with Hypotheses 1 and 2 were the most important we observed, patterns consistent with Hypothesis 4, relating to posteruption geomorphic processes, were also very important. In most areas, steeper slopes had greater revegetation for all response variables. Erosion on steep slopes might affect revegetation by (1) reducing the thickness of volcanic layers covering survivors and organic soils; (2) creating rills and gullies that provide improved microsites for trapping windblown seeds and providing increased shade and moisture; and (3) breaking the crust covering volcanic deposits, thereby enhancing seedling establishment. The importance of slope gradient on revegetation has been noted in field studies at Mount St. Helens (Franklin et al. 1988), although not previously quantified. Research at other volcanoes has been consistent in finding that tephra erodes from steeper slopes and tends to persist on flatter slopes, and that erosion facilitates recovery of surviving vegetation (e.g., Taylor 1957, Eggler 1963, Beard 1976). Although one plot-based study found tephra thickness sometimes significant, but not slope gradient (Halpern et al. 1990), that study measured tephra thickness at the time of the study, not initial thicknesses. Thus, erosion and deposition already had taken place and been accounted for in the measurements. In contrast, our study used

FIG. 5. At the edge of the Plains of Abraham, where primary succession is taking place, faster initial revegetation is evident in gullies on steeper slopes.

initial average tephra thickness as an explanatory variable.

Contrary to our expectations, slope gradient was also very important for primary succession. In these areas, slopes steeper than 18–20° reached EC10 sooner, had greater MEC, and experienced greater TIC (except for 387 ha at the forested edges of mudflows). The importance of slope gradient for primary succession had not been well documented prior to this study. Mechanisms favoring revegetation on these steeper slopes, however, have been observed. Germinating seeds have difficulty in breaking through crusts at the surface of volcanic deposits (Frenzen and Franklin 1985). Water erosion on steeper slopes can break this crust and help seedling establishment. Further, rills and gullies, which are more likely to form on steeper slopes, provide relatively safe areas for seedling germination and establishment (del Moral and Bliss 1993), with potentially increased wind protection, shade, and soil moisture. The importance of gullies on steeper slopes for revegetation at primary successional sites is readily observed at Mount St. Helens (Fig. 5).

Elevation was generally not important, except with respect to later responses (MEC) in secondary successional areas. We hypothesize that dominant species might be shifting in these areas, with dominant species toward the end of the study being more variable with respect to elevation. Resolution of this issue will require finer-scale studies because our study could not distinguish species.

The unimportance of topographic aspect and exposure to the blast might be partially a function of the directionality of the blast. The blast was directed to the north of the crater, and as a result aspect and exposure to the blast are somewhat correlated with disturbance type. Because the regression trees first accounted for variability associated with disturbance type, correlated variables likely would not be significant in lower portions of the regression trees.

Numerous factors prevented higher levels of explanatory power for the regression trees. These factors can be categorized as (1) data quality driven and (2) biogeologically driven. Factors related to data quality included (1) estimation of vegetation cover (the regression formula used to convert satellite spectral bands to Estimated Cover explained 75% of the variation in vegetation cover estimated from aerial photographs), (2) unquantified errors in radiometric and geometric normalizations performed to compare year-to-year satellite images, (3) unquantified errors in GIS layers used to compute explanatory variables, and (4) lack of perfect fit of change curves to time-series data.

Perhaps equally important were biogeological factors not modeled by our explanatory variables. For example, recent research at other sites has established the importance of stochastic factors in successional processes (Vitousek and Walker 1987, Halpern and Franklin 1990). Previous studies at Mount St. Helens have attributed unexpectedly large amounts of variability in revegetation to stochastic factors (Franklin et al. 1985, del Moral and Bliss 1993). Because of lack of data, we were not able to model, for example, the effects of snow cover at the time of the eruption, wind patterns during the study period, localized differences in precipitation, or variability in year-to-year seed production within the surviving forests surrounding the devastated area. Yet each of these factors could have had large effects on revegetation.

Landscape-scale studies, such as this, cannot replace ground-based observations, but they tell us whether processes observed at finer scales result in expected landscape-scale patterns. In turn, landscape-scale studies can indicate needs for further ground-based research. Among other topics, our findings indicate the need for a better understanding of the impact on revegetation of post-eruption geomorphic processes, species-specific seed dispersal mechanisms, and shifts in species dominance over time. Resolving these questions will be accomplished best by examining revegetation at diverse scales over which ecological processes occur.

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