CHAPTER 5

EFFECTS OF CLIMATE VARIABILITY ON *Linaria vulgaris* INVASION IN THE WEST YELLOWSTONE AREA.

ABSTRACT

Alien plant invasions are dynamic processes affected by climatic variability. Anomalies in precipitation and temperature regime can modify the overall environmental conditions, triggering the expansion or retraction of invasive populations. In the West Yellowstone area, expansion in the landscape distribution and infilling of populations of *Linaria vulgaris* has been observed during the last decade, but no data has been collected systematically to report changes over time. This paper aims to describe the variation over a three year period of *Linaria vulgaris* invasion and its effects on plant community at two scales: clonal patch scale and stand scale. *Linaria vulgaris* invasion and its effects were monitored in a three-year period at two spatial scales: stand and clonal patch. At the stand scale, short distance dispersal processes, infilling of infestations and interactions with local site characteristics were studied using. a macroplot of 50 by 100. At the clonal patch scale a 20 by 50 cm sample unit was used to evaluate population structure inside the patches, development of clonal patches, and the interaction of *L. vulgaris* with native vegetation. Spatial patterns of *L. vulgaris* patches at the stand scale appear related to stages of invasion. However, it appears that our 3 year effort was not sufficient in detecting temporal changes in spatial patch distribution with the exception of a new clearcut site. Analyses of radial growth by period suggest that there was a lower growth rate of *L. vulgaris* patches in the 2001-2002 period. that was correlated with drier more difficult growing conditions. Annual variation appears as a significant factor for most of the variables studied at the microplot scale (MANOVA repeated measures, $p < 0.01$). Climate variation appears to be closely associated with changes the density of reproductive ramets; in drier springs less reproductive ramets are produced. This study illustrates the importance of monitoring invasive species in order to understand the ecological implications of invasions. This interannual variation may have more ecological importance in areas with harsh climatic conditions that are limiting to plant growth, as in high elevation protected areas.

INTRODUCTION

Alien plant invasions are dynamic processes affected by climatic variability (Cousens and Mortimer 1995, Bazzaz 1996). Temporal changes in climatic conditions can be a key factor in determining the extent and impact of invasions. Understanding the effect of climatic variability on invasion process may help to identify the environmental conditions which determine invasion success (Dukes and Mooney 1999). Climatic variability also affects invaded natural communities, influencing their susceptibility to invasion and its impacts (Dukes and Mooney 1999).

Climatic variability is usually related to the spatial scale at which processes are occurring. For example, at global scale, climate is relatively stable and they only fluctuate with major global climate changes as has been shown with global warming. However, at regional or local scales, fluctuations in climate patterns can be observed in decades or years. Climatic cycles as El Niño and la Niña modify local climate patterns. At these smaller scales, annual climatic variability may be one of the most important drivers of environmental change.

Anomalies in precipitation and temperature regime can modify the overall environmental conditions, triggering the expansion or retraction of invasive populations (Davis et al. 2000). Even though, environmental variability has been recognized as a driving factor of invasion, much of the research has focused in capturing invasions at a specific point in time (snapshot) with little attention to annual variation in climate (Mack 2000). Monitoring efforts are scarce and usually limited to the extent of grants or the duration of graduate studies (Mack 2000). At regional scales, some efforts utilized herbaria and historical information to trace the development of invasions in long term scenarios (Toney et al. 1999, Arroyo et al. 2000). However, at the local scale most studies are not continued through time. In cases where permanent plots have been located and remeasured, new insights often emerge. For example, in New Zealand, data from permanent plots was instrumental in confirming the consistent expansion of *Hieracium lepidulum* in the understory of *Nothofagus* forests (Wiser et al. 1998).

Linaria vulgaris, a noxious invader of high elevation and cool environments, has been observed increasing its distribution and density in the area around West Yellowstone, Montana (Chapter 4). The species already has invaded disturbed areas in the Gallatin National Forest and is threatening to invade natural ecosystems such as riverbanks, grasslands and shrublands where has already been able to establish, in both Gallatin NF and Yellowstone National Park.

In the West Yellowstone area, expansion in the landscape distribution and infilling of populations of *Linaria vulgaris* has been observed during the last decade, raising the awareness of managers in both conservation units (Chapter 4). However no data has been collected systematically to report changes over time. For these reasons, *Linaria vulgaris* in this area represents a unique opportunity to understand the responses of invasions to high elevation environments in relation to temporal variability.

This paper aims to describe the variation over a three year period of *Linaria vulgaris* invasion and its effects on plant community at two scales: clonal patch scale and stand scale. This chapter complements the findings of chapter 4 by considering changes over time in *L. vulgaris* invasion in the West Yellowstone area. I will describe *L. vulgaris* invasion at the stand and patch scales over three sampling seasons and correlate observed trends with climatic variability, focusing both in the spatial arrangement of patches and in population and community characteristics. I hypothesize that *Linaria vulgaris* and the invaded community presents a strong interannual variation that is associated with annual climatic variation. I expect that this study will help document the value of multi-year monitoring of invasive plants.

Study area

The study area is the same as in chapter 4, located in the Madison Valley around the western entrance of Yellowstone National Park and the adjacent Gallatin National Forest (44˚48'N, 111˚12'W and 44˚37'N, 111˚00'W). A complete analysis of the study area and the biology of *Linaria vulgaris* is presented in chapter 4.

METHODS

  Linaria vulgaris invasion and its effects were monitored in a three-year period at two spatial scales: stand and clonal patch. Each scale was defined arbitrarily to capture a unique set of processes, and specific methods were developed for each scale (described in chapter 4). At the stand scale, short distance dispersal processes, infilling of infestations and interactions with local site characteristics were studied using. The sampling size unit was defined as a macroplot of 50 by 100 m, sufficient to evaluate the structure and dynamics of groups of clonal patches. The patch scale was defined by the size of clonal patch, which varies from 0.5 to 25 m, using a 20 by 50 cm sample unit. At this scale, processes evaluated included population structure inside the patches, development of clonal patches, and the interaction of *L. vulgaris* with native vegetation.

Data Collection

Stand scale

  In August of 2000, we recorded spatial attributes of *L. vulgaris* patches in five macroplots of 100m by 50m (chapter 4). In the Gallatin NF, three macroplots were located in old clearcuts (ca. 20 yr old), and one in a newer clearcut (ca. 6 yr old). In Yellowstone NP one macroplot was located on a riverbank of the Madison River. The three macroplots in old clearcuts were randomly selected from areas logged between 1978 and 1982 with high levels of *L. vulgaris* infestation. In late August of 2001 and late August of 2002, positive or negative radial (horizontal) growth in previously-measured patch axes was recorded for all patches in macroplots. New patches in macroplots were added to the spatial data. Spatial datasets in ArcView were created using the monitoring data.

Clonal patch scale

In August of 2000, patches were randomly selected within each macroplot to locate a set of 50 by 20 cm microplots in randomly selected *L. vulgaris* patches (described in chapter 4, Daubenmire 1968). Microplots were marked permanently using metal stakes. In each microplot, every ramet was recorded along with its height class (10 cm) and reproductive stage (vegetative, reproductive) based on the presence of reproductive structures. In addition, we estimated cover class for each plant species using the five cover classes of Braun-Blanquet (described in Mueller-Dombois and Ellemberg 1974). Microplots were remeasured in August of 2001 and August of 2002.

Analyses

Stand scale

To assess changes in spatial patterns, we conducted point pattern analyses in the 2000 and 2002 macroplot data. Analyses were run for four macroplots, two in old clearcuts under severe invasion, one in a newer clearcut at early stages of invasion, and one in a riverbank of Yellowstone NP. Distribution patterns in patch centroids within macroplots were estimated Ripley's K statistic and Duncan's (1990) statistical program. The Ripley's K method compares the number of points that fall in a circle as a function of diameter and compare the function with the 95% confidence interval of random runs using MonteCarlo simulation. Results for 2000 and 2002 were compared to explore the possibility of detecting changes in spatial patterns in the short-term (2 years). In addition, area covered by *L. vulgaris* patches, mean patch size and total number of patches were calculated for each macroplot by year.

The role of year and macroplot in determining patch radial growth was tested using ANOVA and t-test for pairwise comparisons among years (judged significant when $p<0.05$). The effect of patch diameter in determining annual radial was tested using a linear model (significant when $p<0.01$) for each of the two periods studied (2000-2001 and 2001-2002).

Clonal patch scale

MANOVA repeated measures was used to test for the effect of annual variation in *Linaria vulgaris* and the invaded community. In medium and large patch combined of old clearcuts (N=12 patches, n=84 microplots), we tested for the effects of year of measurement (2000, 2001, 2002) and its interaction with location in the patch (outside, edge, interior, center) and macroplot in microplots variables. Microplot variables (dependent variables) tested included *L. vulgaris* attributes (total ramet density, vegetative ramet density, reproductive ramet density, cover %, biomass, maximum height, average height), and community attributes (total cover % of other plants, species richness, and species richness without considering *L.vulgaris*). Density, biomass and cover variables were transformed using lognormal. In addition, for each year, MANOVA was used to determine the effect of position and macroplot in these microplot variables. Biomass was calculated using a regression curve with plant height obtained from 80 individual samples homogenously distributed from 0 to 80 cm and randomly chosen from old clearcuts in August of 2002 (R^2=0.92, p<0.001, Height=b*biomass[1/3]).

To test for changes in the correlation between *L. vulgaris* attributes and the invaded community in old clearcuts, linear models were run for each of the three sampling period datasets. For all microplots in old clearcut patches (N=114), including small, medium and large patches (N=18), correlation between species richness and other plant cover vs. *L.vulgaris* density, cover and biomass were tested using single variable linear regression models.

To detect temporal changes in the new clearcut and the riverbank macroplots, microplot variables were graphically displayed using standard errors, but due to the lack of replicates, not statistical analyses were conducted.

Climatic variation

To find correlation patterns between annual climatic variation and *Linaria vulgaris* invasion, climate data was analyzed for the three years of data collection and compared with climate averages (normals) for the last 107 years (1895-2002). Data was obtained for the Yellowstone Drainage climate division (Western Regional Climate Center 2002). Weather data was not available for the study site due to discontinuity on the records of the West Yellowstone weather station. Variables were analyzed as monthly averages and included mean daily temperature (C) and precipitation (mm). Anomalies for the historical monthly average were compared among the three-year period. Data was interpreted by correlating anomalies with significant changes in *L. vulgaris* and the invaded community at the stand and patch scales.

RESULTS

Stand scale

Results from the Ripley's K tests indicated that in 2000, *Linaria vulgaris* patches showed a random distribution at all distances in old clearcuts, and in the riverbank site (Table 1, Fig. 1, Fig. 2). Patches in the new clearcut showed clumpiness between 0 to 15 m, being ramdonly distributed at longer distances (Fig. 2). The old clearcut and riverbank macroplots showed no change in spatial arrangement during the two year period, however the new clearcut tended to be more randomly distributed in 2002 than in 2000 (Fig. 2).

Year and macroplot were both significant in determining radial growth (ANOVA, p<0.001). Radial growth was higher during the period 2000-2001 than the period 2001-2002 for all macroplots, but t-tests showed significant differences for only one old clearcut macroplot (Fig. 3). For old clearcuts, no significant relationship was found between patch diameter and radial growth at neither period (linear regression, p>0.05).

Total area cover by *L. vulgaris* increased from 2000 to 2002 in all macroplots, however the number of patches was reduced in new clearcuts (Table 1, Fig. 4). A trend towards increased

patch size was observed, but was influenced by the formation of smaller new patches, which lowered the mean size. In old clearcuts the total coverage of *L. vulgaris* patches approaches 18%, while in new clearcuts and the riverbank is only ca. 2% (Table 1).

Clonal patch scale

In medium and large patches within old clearcuts, year was a significant factor in most of the microplot variables (Table 2, Fig. 5). For four variables, the interaction year*position (in the patch) was significant. However, for only biomass and height the interaction year*position*macroplot was significant, while the interaction year*macroplot was not significant for any variable. For the new clearcut and the riverbank, variables showed much higher variation when compared to old clearcuts (Fig. 6).

MANOVA analyses for each year showed that position was a significant factor in most microplot variables, while macroplot and the position*macroplot interaction was rarely significant (Table 3). Significant variation in the model and explanatory factors by year was observed in other species total cover and species richness without *L. vulgaris*.

Weak relationships were found among species richness and other plant total cover vs. *L. vulgaris* density, cover, height and biomass (Table 4, Fig. 7). However, *L. vulgaris* height was the best predictor for other species total cover and maximum height was the best predictor of species richness w/out *L. vulgaris*. No variable was significantly correlated to species richness when considering *L. vulgaris*. Minor changes, from year to year, were found in model precision (R^2), but no clear trend was evident.

Climatic effects

Spring of 2000 was wetter than normal, but summer was drier than normal (Fig. 8). However, 2001 had close to average precipitation for spring and summer drought with deficit of precipitation in previous winter months. Precipitation for the year 2002 was lower than normal

for winter, spring and summer. For the three years, winters and summers were dryer than normal and much of the inter-annual variation occurred in spring.

Mean temperatures were on average higher than normal for the three-year period in all seasons. Only 1999 and 2002 appear closer to normal records during spring, reporting cool temperatures between April and June.

The wetter than normal spring of 2000 is associated with the highest values for reproductive ramet density, species richness, and other species total cover (Fig. 5). All these variables decreased in 2001 and 2002. Most microplot variables show a similar response in 2001 and 2002, however reproductive ramets diminished abruptly in 2002. During 2002, few plants reached reproductive maturity and visual observations showed a low percentage of ramets producing floral structures and even fewer containing viable seeds. In microplots located in patches edges and outsides, the negative effects of climate variation were compensated by intrinsic patch growth (Fig. 5). Patch edges still show growth regardless of climatic variations. However, the drier than normal 2002 growing season was associated with a decrease in the rate of radial patch growth compared to previous growing season (Fig. 4). No clear pattern emerged between temperature and *L. vulgaris* and the invaded community variables, mainly because all years showed higher than normal temperatures.

DISCUSSION

Stand scale

Spatial patterns of *L. vulgaris* patches at the stand scale appear related to stages of invasion. Early stages of invasion show a clumped distribution that may be caused by insufficient propagule dispersal. However, as *L. vulgaris* increases its abundance, as in old clearcuts, its patches become randomly distributed. These results confirmed preliminary statistical analyses of this data (chapter 4). It appears that the 3-year effort was not long enough to detect temporal changes in spatial patch distribution with the exception of the new clearcut site. These results

suggest that processes of expansion and structuring of patch arrangement in *L. vulgaris* can take several years or decades, demanding a longer term monitoring effort.

However, I was able to detect changes in the overall coverage of patches by determining radial growth. As it appears, old clearcut infestations are still growing in abundance covering over 16% of the total area, adding ca. 1% annually (Table 1). In the case of riverbanks and the new clearcut, the coverage is much lower (ca. 2%) but increasing a proportionally higher rate (Table 1). Our method presented some limitations in addressing changes in patch shape and aggregation of adjacent patches (see field methods in chapter 4). These limitations probably did not have major implications in estimating patch structure in this short term monitoring, because most patches did not change drastically their shape. However, improvement in the field method is required for longer-term monitoring.

Analyses of radial growth by growing season suggest that there was a lower growth rate of *L. vulgaris* patches in 2002. These changes are consistent across landuses suggesting that climatic variations or other landscape phenomena are determining growing patterns. As mentioned before, the growing season of 2002 presented more difficult growing conditions for *L. vulgaris*, which could explain the decrease in radial growth, especially considering that *L. vulgaris* has been shown to have higher invasion success on wet and cool environments (Saner et al. 1995).

Clonal Patch scale

Annual variation appears as a highly significant factor for most of the variables studied at the microplot scale. Interestingly, total ramet density is not significantly affected by yearly variation. However, when analyzed separately, both reproductive and vegetative ramet densities are related to yearly variation. This suggests that intrinsic population growth and reproductive effort may be interacting. The relationship between spring precipitation and the number of reproductive ramets suggests that climate variation may be responsible for changes in

reproductive effort. On the other hand, vegetative ramets could be less sensitive to climatic variation, which would explain the continuous vegetative growth of patches (Fig 5).

Year does not significantly correlate with biomass changes, but the interaction of year and position and the interaction of year, position and macroplot are significant. This suggests that biomass is more sensitive than density to specific site conditions. In this case, it appears that the decrease in height and density during the last two years in the interior and center plots contrasted to the increasing trend for these variables at edge plots.

Changes in height, density and biomass also appear associated with macroplot, which was an indirect indicator of site differences between old clearcuts. When analyzed by year, position is consistently a significant factor in explaining biomass.

A significant annual variation in species richness ($p<0.01$), with an overall decrease in 2001 and slight recovery in 2002 (Fig. 5), illustrates that the invaded community may also be influenced by climatic variation. In the three-year period, species richness was not related to position in the patch, indicating no effect of *L. vulgaris* in overall diversity. (Tables 2, 3). Similarly to *L. vulgaris* cover, other species total cover decreased consistently during the three-year period even in outside microplots not affected by the invasion, suggesting major effects of climatic variability. These results suggest that while *L. vulgaris* tends to diminish cover of other species, it has little effect on the overall species number.

The displacement of native species however, is not clearly expressed in the relationship between native species richness and other species total cover, versus *L. vulgaris* attributes. I interpret these results as evidence that there may not be direct competition for resources between native plants and *L. vulgaris* and therefore, their abundance and overall diversity is mainly constrained by other abiotic and biotic factors. For example, observed changes in reproductive effort may also be a product of the interactions between climate variability and herbivores, which in the case of *L. vulgaris* effect strongly reproductive structures (Saner et al. 1995).

Monitoring invasions

This study illustrates the importance of monitoring invasive species in order to understand the ecological implications of invasions (Mack 2000). A one time "snapshot" could provide partial and misleading information about the invasion process. For example, with one-year observation I could have concluded that *L. vulgaris* was an extremely vigorous invader with high seed production.

The multi-year effort allowed me to detect short-term annual variation, which could have profound effects in the overall invasion success. It appears that *L. vulgaris* is remarkably sensitive to climatic changes and that these could explain, at least partially, why it has not been shown to be a consistently aggressive species (Saner et al. 1995). Also, this annual variation seems not to only affect the invader, but also the native community (e.g. species richness, plant cover). The interaction between both invader and native species and annual cycles may be crucial to understand the elements that define years of high invader recruitment and population expansion or years of retraction. Climate may influence the potential of the invader but also the susceptibility to invasion of the native community. I found that for *Linaria vulgaris* sensitivity to annual climatic variation is primarily related to changes in precipitation patterns rather than changes in temperature regimes. This data are consistent with the widely held view that water availability is a key constraint to vegetation growth in this harsh environment (chapter 4).

Interannual variation may have greater ecological importance to areas with harsh climatic conditions that are limiting to plant growth, as in high elevation protected areas. Fluctuations in climatic factors could define the outcome for alien species populations in these extreme environments. This environmental variability may also stimulate cyclical behavior of invasive populations with wide implications in terms of their impacts and their management. In these sensitive environments, global warming can also worsen the effects of invaders by altering precipitation and temperature patterns (Dukes and Mooney 1999).

This study, by focusing on short term monitoring, alludes to the potential value of longer term monitoring efforts in plant invasions. The observed short-term trend of slower expansion of *L. vulgaris* in adverse conditions may be reversed in the long term if climatic conditions change. If the goal is to understand and manage invasions, monitoring efforts should follow a similar scheme to that of a multi-scale assessment (chapters 1, 4). Different temporal windows should be used to study invasion processes, which should allow us to capture a broader range of phenomena related to the invasion process.

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Table 1. Annual summary of stand scale attributes for four macroplots. Values correspond to 2000, 2001 and 2002 measurements. Spatial distribution based on Ripley's K function (R= random, C= clumped).

Macroplot	Patch number	Mean Patch Size (m^2)	Total Area (%)	Mean Radial Growth	Spatial Pattern 2000	Spatial Pattern 2002
Old clearcut 1	29 | 33 | 34	26.3 | 25.9 | 27.5	15.3 | 17.1 | 18.7	24.20 | 23.91	R	R
Old clearcut 2	17 | 19 | 19	45.8 | 46.0 | 44.2	15.6 | 16.6 | 16.8	16.08 | 5.65	R	R
New clearcut	10 | 9 | 6	6.7 | 9.7 | 16.9	2.8 | 3.4 | 3.7	32.78 | 19.79	R./C	R
Riverbank	8 | 8 | 8	17.7 | 21.0 | 23.3	1.3 | 1.7 | 2.0	28.50 | 16.29	R	R

Table 2. MANOVA repeated measures for microplot variables in large and medium patches of old clearcuts (N=18 patches, n=84 microplots). Factor are year (Y: 2000, 2001, 2002), macroplot (M) and position in the patch (P: outside, edge, interior, center). Values indicate significance of relationship.

Variable	Year Factor (p)	Y*P Interaction (p)	Y*M Interaction (p)	Y*P*M Interaction (p)	3Y average-Position (p)
Linaria vulgaris **attributes**					
Ramet density (log10)	0.091	n	n	n	0.000
Reproductive ramet density (log10)	0.000	0.006	n	n	0.000
Vegetative ramet density (log10)	0.000	n	n	n	0.000
Linaria vulgaris cover (log10)	0.029	n	n	n	0.000
Linaria vulgaris biomass (log10)	n	0.007	n	0.001	0.000
Average Height	0.000	0.008	n	0.019	0.000
Maximum Height	0.000	0.000	n	0.000	0.000
Community attributes					
Other species cover (log10)	0.000	n	n	n	0.021
Species richness	0.000	n	n	n	n
Species richness w/out *L.vulgaris*	0.000	n	n	n	0.026

Table 3. ANOVA, by year, for microplot variables in large and medium patches of old clearcuts (N=18 patches, n=84 microplots). Factor are year macroplot (M) and position in the patch (P: outside, edge, interior, center). Macroplot and Macroplot*Position interaction were never significant. SS: sum of squares, F: F value, p: probability of significance, R^2: R squared for the model.

Variable	Year	Corrected SS	Model F	p	Position SS	Factor F	p	Error SS	R2
Lnaria vulgaris attributes									
Ramet density (log)	2000	38.80	15.0	0.000	37.52	53.2	0.000	16.92	0.70
	2001	43.07	13.5	0.000	41.66	48.0	0.000	20.84	0.67
	2002	37.02	14.8	0.000	36.51	53.7	0.000	16.33	0.69
Reproductive ramet density (log)	2000	39.10	10.2	0.000	35.33	33.8	0.000	25.10	0.61
	2001	25.92	5.2	0.000	24.71	18.2	0.000	32.54	0.44
	2002	13.59	2.7	0.006	11.89	8.7	0.000	32.82	0.29
Vegetative ramet density (log)	2000	55.49	37.7	0.000	54.02	134.5	0.000	9.64	0.85
	2001	53.45	20.9	0.000	52.39	75.1	0.000	16.75	0.76
	2002	42.67	17.6	0.000	42.42	64.2	0.000	15.87	0.73
Cover (log)	2000	23.11	14.8	0.000	22.38	52.5	0.000	10.23	0.69
	2001	20.28	10.8	0.000	19.86	38.7	0.000	12.32	0.62
	2002	16.99	11.3	0.000	16.42	40.1	0.000	9.82	0.63
Biomass (log)	2000	44.26	21.0	0.000	41.69	72.5	0.000	13.80	0.76
	2001	31.47	12.1	0.000	30.32	42.8	0.000	17.00	0.64
	2002	28.95	15.3	0.000	28.24	54.6	0.000	12.41	0.70
Average Height	2000	8568.68	11.8	0.000	7818.37	39.6	0.000	4739.19	0.64
	2001	4703.90	5.5	0.000	4230.12	18.1	0.000	5611.23	0.46
	2002	4169.80	9.8	0.000	4027.30	34.5	0.000	2798.80	0.60
Maximum Height	2000	25657.14	12.6	0.000	23640.48	42.5	0.000	13350.00	0.66
	2001	13985.42	7.6	0.000	12981.25	25.7	0.000	12106.25	0.54
	2002	10866.07	8.4	0.000	10207.74	28.9	0.000	8487.50	0.56
Community attributes									
Other species cover (log)	2000	7.07	2.3	0.020	3.46	4.1	0.010	20.41	0.26
	2001	5.56	1.6	0.130	2.36	2.4	0.073	23.35	0.19
	2002	5.55	1.9	0.049	2.69	3.4	0.022	18.82	0.22
Species richness	2000	35.66	1.0	0.441	12.24	1.3	0.288	229.63	0.13
	2001	27.56	1.0	0.450	8.73	1.2	0.328	179.25	0.13
	2002	30.81	1.2	0.312	4.73	0.7	0.575	170.00	0.15
Species richness w/out _L.vulgaris_	2000	32.19	0.9	0.514	9.10	1.0	0.413	225.63	0.13
	2001	49.81	1.9	0.048	32.73	4.7	0.005	168.00	0.23
	2002	49.24	2.0	0.039	23.16	3.5	0.020	160.00	0.24

Table 4. Changes in R^2 in regression for variables in all microplots of old clearcuts (n=114). Community attributes (a. other species total cover, b. species richness and c. species richness without *Linaria vulgaris*) vs. *L.vulgaris* attributes (ramet density, cover percentage, maximum height and biomass).

Variable\ *Linaria vulgaris*	Density (log)	Cover (log)	Max. height	Biomass (log)
a. Other species total cover	0.14 | 0.13 | 0.07	0.12 | 0.16 | 0.12	0.13 | 0.15 | 0.11	0.14 | 0.16 | 0.11
b. Species richness	* | * | *	* | 0.04 | *	* | * | *	* | * | *
c. Spp richness (w/out *L.vulgaris*)	* | 0.10 | 0.06	* | 0.17 | 0.10	0.05* | 0.07 | 0.14 |	* | 0.16 | 0.09
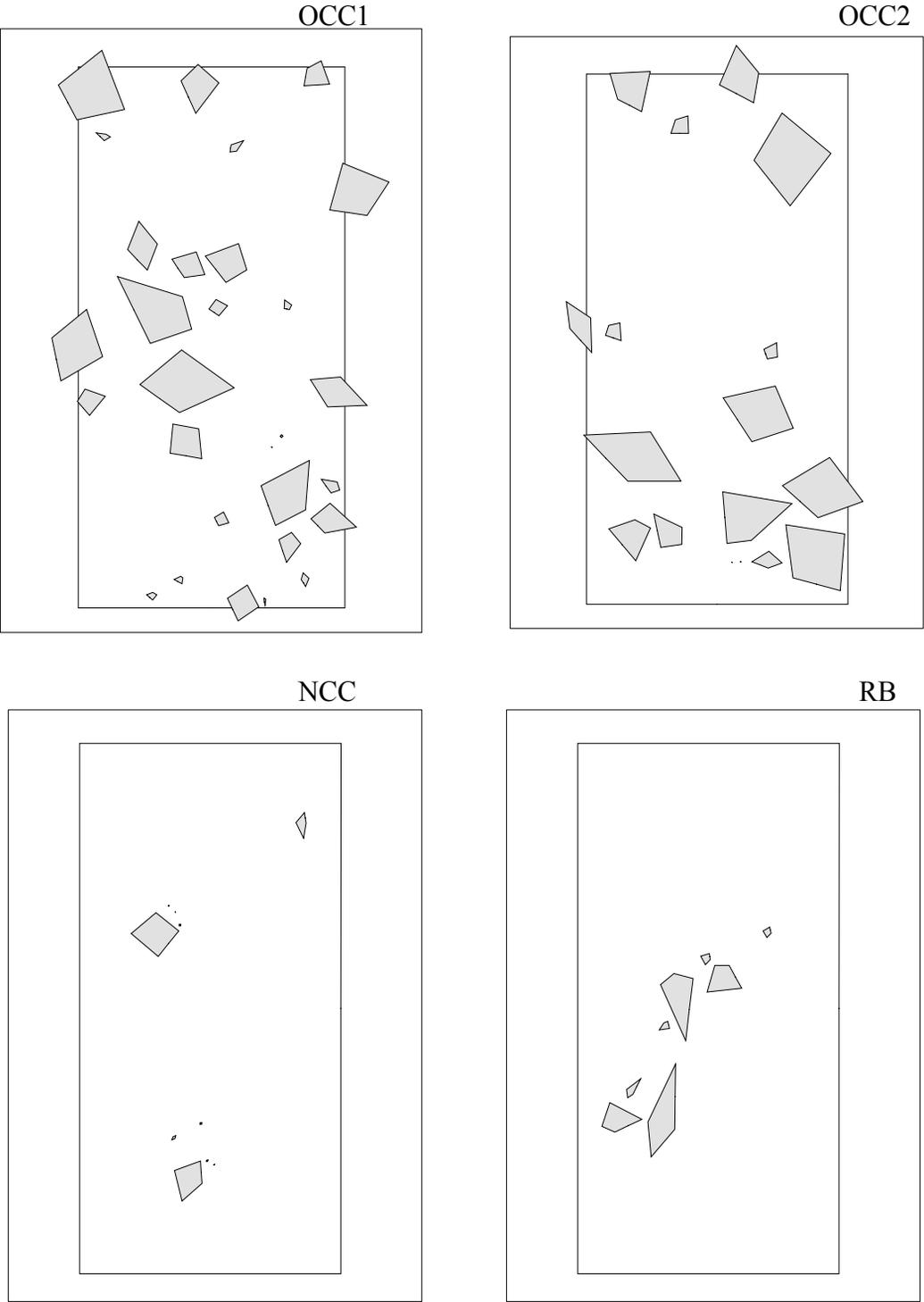
Fig. 1. *Linaria vulgaris* patch distribution at the stand scale for old clearcuts (OCC), a new clearcut (NCC) and a riverbank (RB). Macroplots are 50 by 100 m.
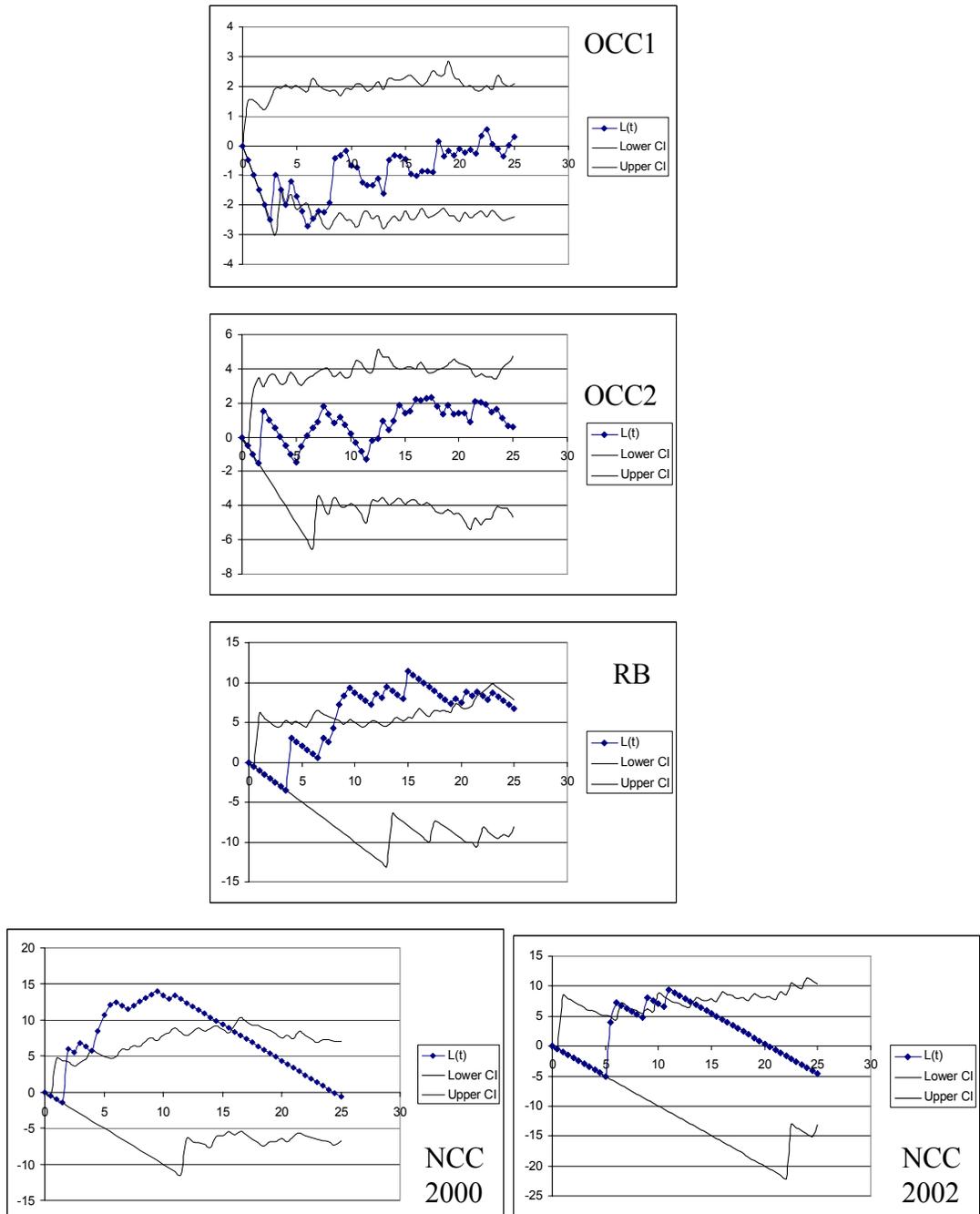
Fig. 2. *Ripley's K* simulation for four macroplots in 2000: two old clearcuts (OCC1, OCC2), one in riverbank (RB) and one in a new clearcut (NCC). A simulation for 2002 is shown for the NCC. L represents the K statistic for a determined distance (t) shown in axis X. Simple lines represent the lower and upper confidence limit at 95%.
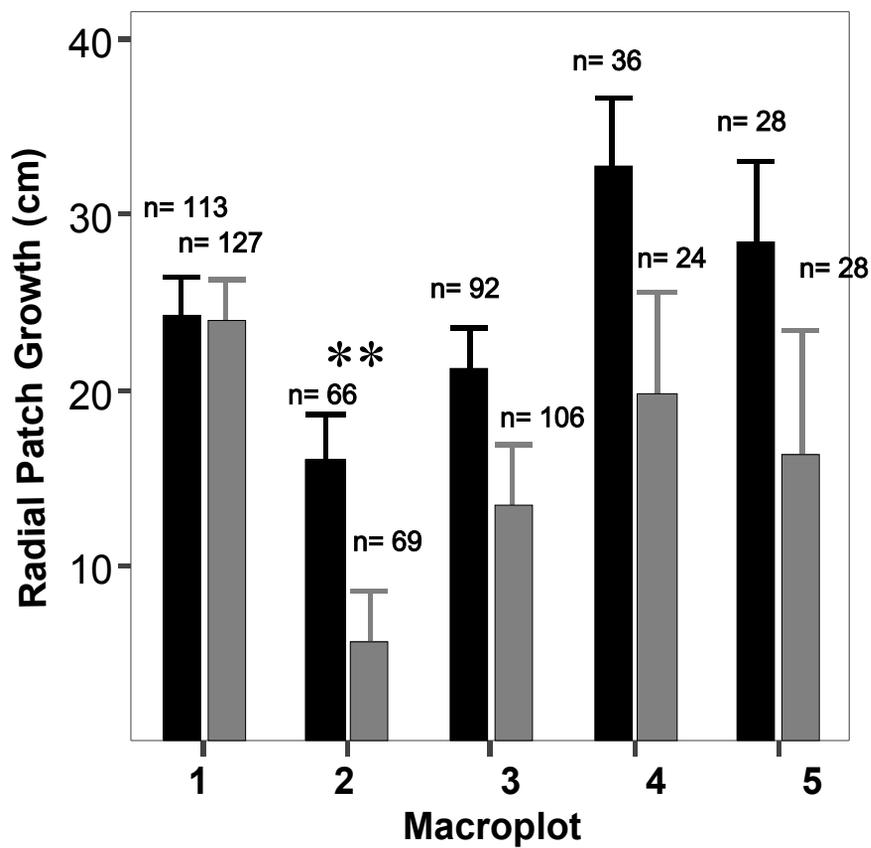
Fig. 3. Radial patch growth for *Linaria vulgaris* in periods 2000-2001 and 2001-2002 by landuse in old clearcuts (1,2,3), a new clearcut (4) and a riverbank (5). N indicates the number of corners used for measuring radial growth. ** indicates significance at $p<0.01$.
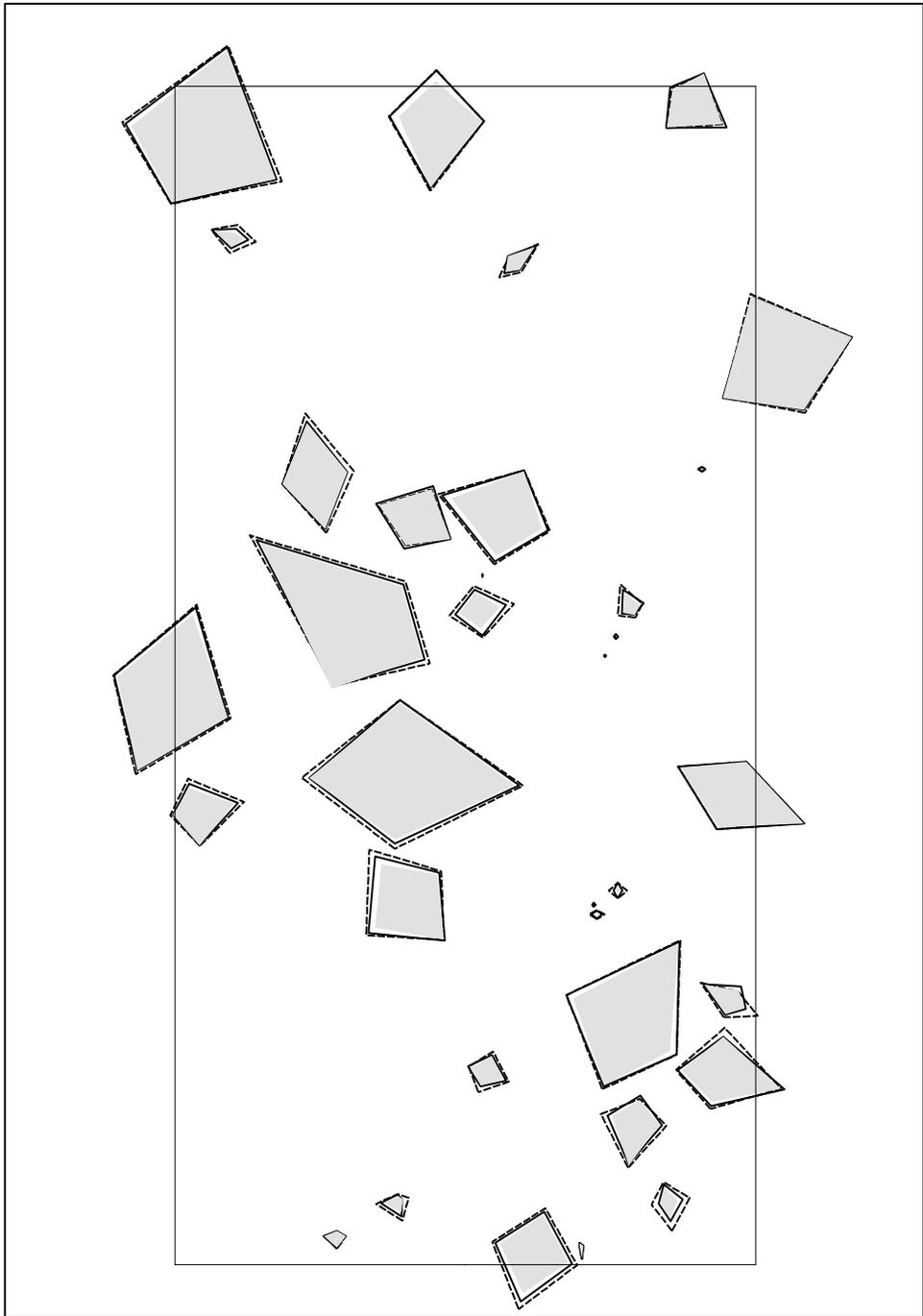
Fig. 4. Temporal changes in *Linaria vulgaris* patch distribution at the stand scale for an old clearcut (OCC1). Grey indicates the initial patch shape in 2000; continuous line indicates shape in 2001; and dashed line indicates shape in 2002. Changes in patch shape were determined using measures of annual radial growth.
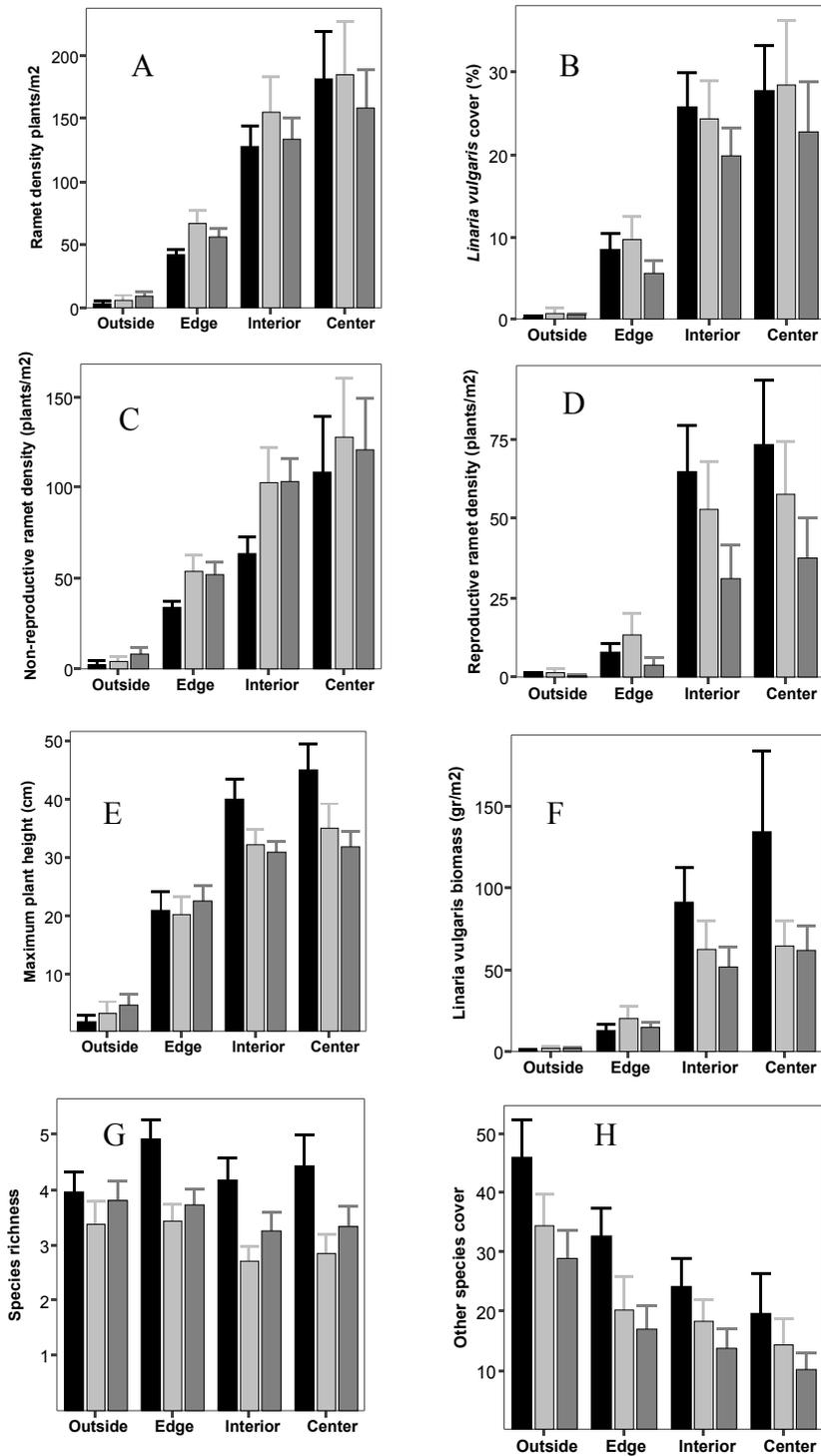
Fig. 5. Mean microplot variables ± SE in old clearcuts by location and year. *Linaria vulgaris* attributes: a) ramet density, b) cover %, c) vegetative ramet density, d) reproductive ramet density, e) maximum height and f) biomass, and community attributes g) species richness and h) other species total cover.
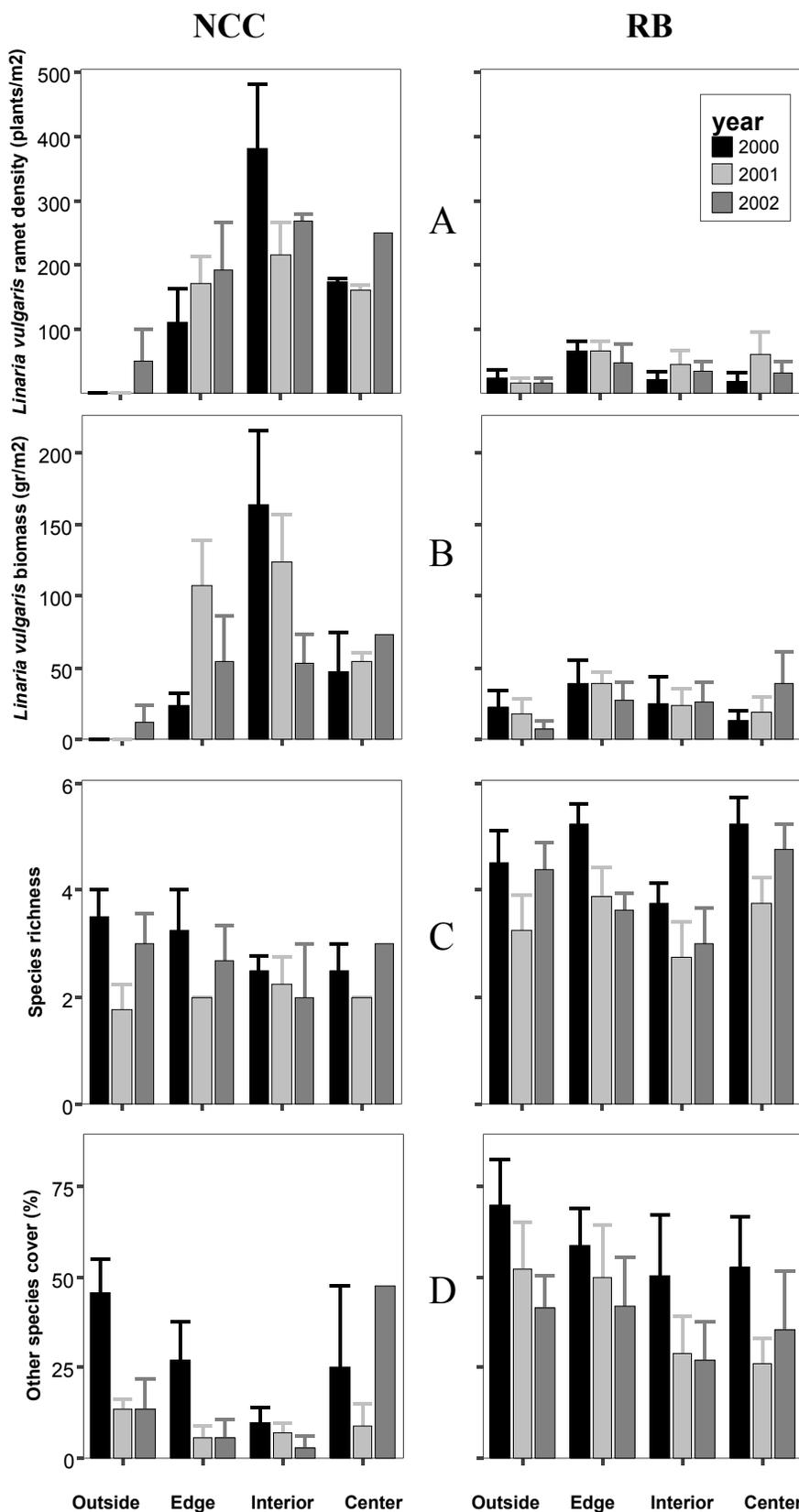
Fig. 6. Mean microplot variables ± SE in new clearcut (NCC) and riverbank (RB) by location and year. *Linaria vulgaris* attributes: a) ramet density, b) biomass, and community attributes c) species richness and d) other species total cover.
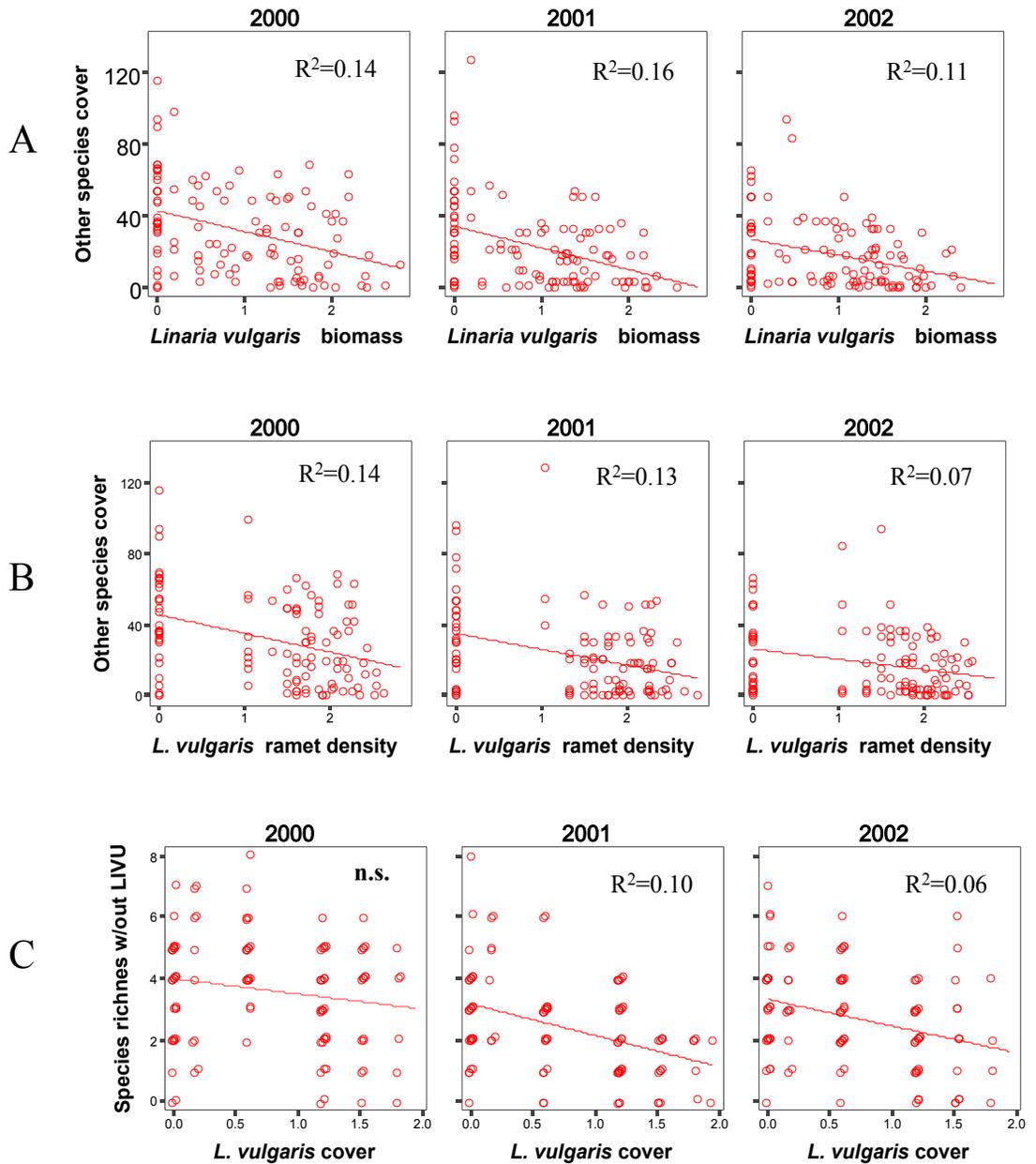
Fig. 7. Regression lines and scatterplots for variables in microplots of small, medium and large patches of old clearcuts combined (N=114). a) Other species cover vs. *L.vulgaris* biomass (log), b) Other species cover vs. *Linaria vulgaris* density (log), c) Richness without considering *L. vulgaris* vs. *L. vulgaris* cover (log). All relationship were significant (p<0.05), except for one (n.s.).
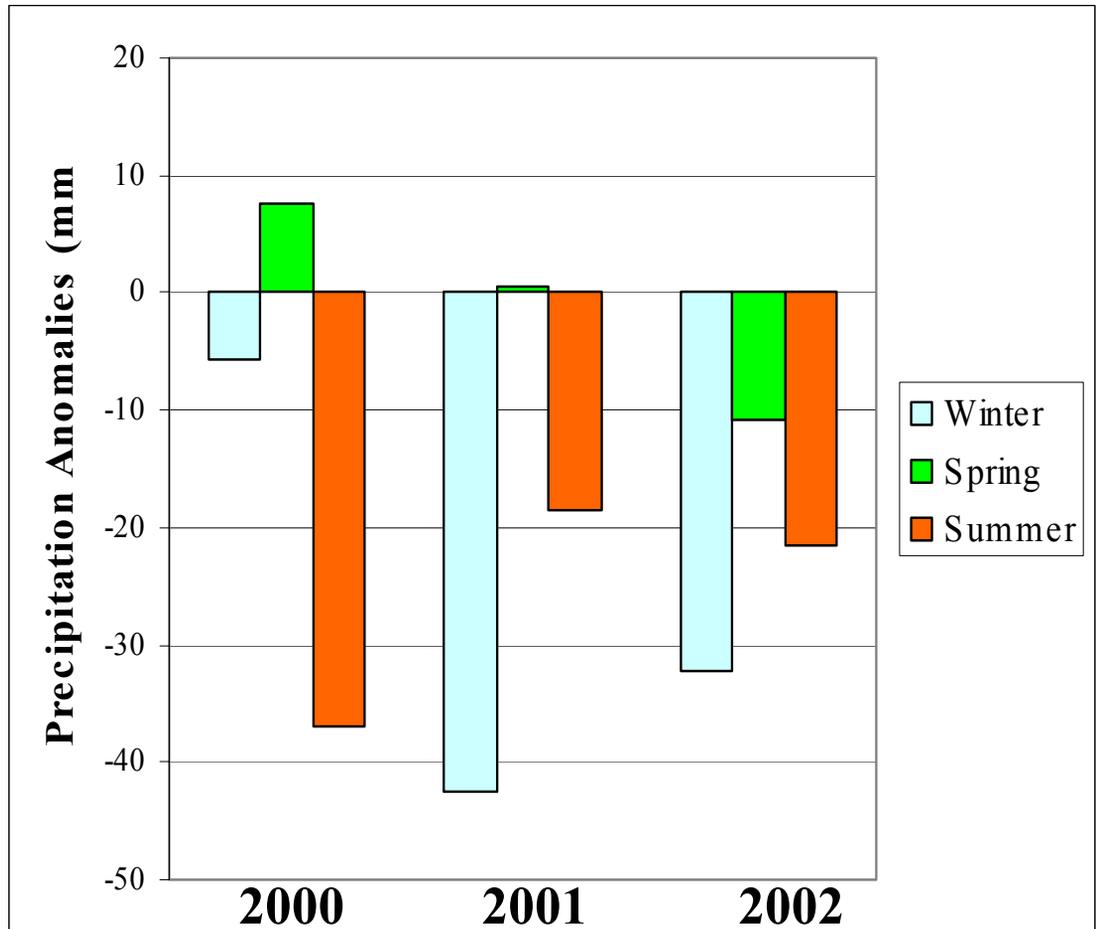
Fig. 8. .Precipitation anomalies from the normal (107 yrs record) for the Yellowstone Drainage climate division during the three years of data collection. Winter precipitation includes January, February, March; Spring includes: April, May, June; and Summer includes July and August.