Effects of Precipitation on Annual Growth Rate in *Populus tremuloides*:

An analysis of genetic variation in growth response to water availability within a population of trembling aspen

By:
Darlene Howery
Lisa Passerello
Andrea Pullo
Hillary Taylor

INTRODUCTION

Survival of a species depends not only on its genetic variation, but also the environmental conditions under which it lives. If environmental conditions change, a species can adapt only to the extent that genetic variation within the species allows. Studies over the last half century suggest a steep rise in the levels of CO_2 and other greenhouse gases that trap some of Earth's heat radiated in the lower atmosphere. The projected result of this greenhouse effect is a long-term increase in the Earth's surface temperature (figure 1). Climate change models designed by the Geophysical Fluid Dynamics Laboratory predict that soil moisture levels in mid-latitude continental areas will decrease substantially as a consequence (figure 2)(GFDL, 1998). Responses of natural populations to such changes in climate may determine the future composition and distribution of species on the planet; for example, reductions in moisture levels may affect the geographic distribution of forest biomes and ecosystems (Wetherald, 1991). If one genotype within a tree species is best able to respond to drier conditions, then natural selection has the potential to favor that genotype and allow the species to survive in the same geographic area. In contrast, if no genetic variation for growth response to water availability exists within a species, then that species's habitat range may shrink.

Water stress can result in a decrease growth of trees. As water becomes scarce, the tree responds by suppressing photosynthesis to avoid water loss through transpiration (Stocker1960; Brix, 1962, in Slatyer 1967). However, with a limited water supply, the tree is unable to store as much water in its vacuoles, and, as a result, cell size decreases. This decrease in cell size is often evident in a tree's annual growth rings; where decreased water absorption has been found to be correlated with a decrease in annual tree growth (Slatyer, 1967). In trembling aspens, *Populus tremuloides*, photosynthetic rates nearly cease around mid-day, when surface temperatures and transpiration rates are highest (Frahm, 1995). In the context of global warming, these findings suggest that, as surface temperatures and rates of evaporation increase, tree photosynthesis may be inhibited and, hence, annual growth rates would decrease over time.

Past research at the University of Michigan Biological Station (Capps *et al.,* 1990), did not find a correlation between precipitation and growth rings of bigtooth aspen, *Populus granditentata,* in either mesic or xeric soil. However, the observed lack of correlation could have resulted if there is clonal variation for growth response to precipitation; their study did not distinguish between clones in its samples.

We studied a population of trembling aspen, *P. tremuloides,* in the Pellston outwash plain of northern lower Michigan (figure 1), in order to address three questions: 1) Do precipitation levels affect growth rates of *P. tremuloides*; 2) Does this population of *P. tremuloides* contain clonal variation for growth response to precipitation; and 3) If so, do certain clones respond better than others to dry conditions predicted under global warming models?

MATERIALS AND METHODS

Study Organism: *Populus tremuloides*

Trembling aspen, a nutrient-, moisture-, and light-demanding species with a large geographic range, was chosen for this experiment for both its abundance and growth pattern (Barnes, 1966). Trembling aspen typically grows in clumps of vegetatively propagated, genetically identical individuals called clones (Graham, 1963). A xeric outwash plain is a particularly appropriate site for our study because aspen diameters are significantly smaller than on a nearby mesic, glacial moraine site, indicating that tree growth on xeric sites may be water-limited (Clyne et al., 1998).

Sample Collection and Preparation

In order to determine whether precipitation affects annual growth rate of *P. tremuloides*, we cored 15 trees from four different aspen clones on the Pellston plain. The clones chosen were located within a 23,225 m^2 area to minimize soil, temperature and precipitation differences (figure 3). Because tree ring width decreases with increasing age

(Schweingruber, 1989), we limited our samples to trees with a diameter at breast height (DBH) of 11-18 cm so that age differences among trees would not complicate our tree ring measurements. To minimize differences in growth that orientation to the sun may cause (Graham, 1963) we cored all trees on their south side.

Prior to measurement, cores were mounted in a wooden groove, sanded, and moistened. Ring widths were measured in tenths of a millimeter using a dissecting microscope.

Relative growth

Ring width within a given tree decreases over time (Braker, 1981 in Schweingruber, 1989). Although we attempted to sample trees of the same size and age, within each clone some DBHs differed by as much as 7cm. Therefore, tree size and age will confound comparisons of absolute ring width. In order to minimize effects of age or size on ring width, we calculated relative growth as follows. Within each tree, ring width was expressed as proportions of that tree's total growth over the past 24-33 years. This proportion indicated that tree's annual growth during a given year, relative to its growth over its entire lifetime, and hereafter will be called "relative growth." We believe relative growth allows more accurate comparisons between trees of different sizes or ages.

Effect of precipitation on annual growth of *Populus tremuloides*

In order to examine whether there is a correlation between annual growth and precipitation within each clone mean annual relative growth was calculated as the average of the relative growth of all trees within a clone. Correlations were then performed for each clone between mean relative growth and precipitation for each of four precipitation variables: 1) spring-summer rainfall (April-August), 2) September-December rainfall, 3) January-May rainfall, and 4) annual rainfall (October-September). Relative growth was also compared to monthly precipitation for every month. Precipitation measurements used were those recorded at the Pellston Airport. If precipitation levels were positively correlated with annual growth, then larger relative ring widths would coincide with years of higher annual rainfall, and smaller relative ring widths would coincide with years of lower annual rainfall.

Clonal variation for response of growth to variability in annual precipitation

In order to examine whether this population contains genetic variation for growth response to variability in annual precipitation levels, we correlated mean annual relative growth for each clone with annual precipitation for the last 24-33 years. An analysis of covariance could then be used to compare the slopes of the precipitation-regression lines among the four clones. Significant differences in the slopes of the regression lines would suggest variation in clonal response to precipitation.

Clonal variation for growth in years of high or low precipitation

To determine whether certain genotypes grow better than others at low soil moisture levels such as those predicted with increased global warming, we compared mean absolute annual ring widths among the four clones by analysis of variance (ANOVA). Separate ANOVAs were performed for each clone in the three years of lowest precipitation since 1964 (1966, 1989, and 1992), and for each of the four years of highest precipitation since 1964 (1972, 1974, 1978, and 1984). To compare if clonal hierarchies were different in low and high precipitation years high precipitation years were also analyzed. To correct for variation in growth due to tree size or age, we ran each ANOVA with DBH as a covariate. If DBH was not significant, ANOVAs without DBH as a covariate were used.

RESULTS

Clonal growth response to variability in annual precipitation

Relative growth was not significantly linearly correlated with annual precipitation for any of the four clones (figure 4). Moreover, only a single clone (clone 29) exhibited a nearly significant non-linear correlation (Relative growth = 1/(933.0791 – 0.270 * annual precipitation), $r^2 = 0.13$, df. = 2, p=0.09).

Similarly, no clone exhibited a significant linear correlation between relative growth and any other precipitation variable (spring-summer, September-December, January-May, and each month separately); to examine which months of precipitation were most correlated with clonal growth we performed a multiple regression and sequentially removed precipitation variables until either the overall p-value began to increase or until all variables remaining were significant. We found that each clone responded most significantly to precipitation in different months (figure 5).

We were surprised to find that, although average growth between clones did not appear to be influenced by precipitation variables, individual trees within clones showed significant and highly varied responses to both annual and monthly precipitation levels (table 1). For example, within clone 51, growth of tree 7 was positively correlated with January precipitation, while growth of tree 12 was negatively correlated with precipitation during the same month.

Since no significant correlations were found for any clone's response to variable precipitation, we were not able to compare regression slopes among clones.

Clonal variation in growth response to high or low precipitation

For all years considered, DBH did not have a significant effect on growth, so we conducted ANOVAs again without a covariate. In both high and low precipitation years, absolute growth differed significantly between clones (table 2, figure 6). Clone 29 grew best in both high and low precipitation years, while clone 50 and 51 did not grow as well as 29 or 43.

DISCUSSION

Global climate change models predict a doubling of atmospheric CO_2 in the next 50 years. Such as change will increase global average surface temperature and decrease soil moisture. As a result, populations will have to adapt quickly to new conditions, disperse to suitable habitats or face extinction. It is important that the scientific community begins to address the consequences of global warming today in order to best plan for the future. Thus far the study of the existence of genetic variation to facilitate adaptation to future conditions has been largely ignored. We examined *P. tremuloides* for such variation.

In our investigation of how precipitation affects growth rate of *P. tremuloides*, we tested our data in three ways. First we compared annual precipitation with growth, and a significant correlation was not found. Aspens may not be affected by future decreases in precipitation because our study suggests the amount of precipitation that they receive each year does not determine how much they grow. On the other hand, precipitation may cause change in growth only if the amount of precipitation is below the water stress point for the trees. Roth *et. al* (1997) found that *P. tremuloides* do not respond to drought conditions until 17 days after the onset of a drought. If droughts in the future do not meet these conditions *P. tremuloides* may continue to not show a change in growth rates.

Second, we found a nearly significant non-linear positive correlation of annual precipitation with growth for Clone 29, which suggests growth of this clone (but not of others) responds positively to an increase in precipitation. However it should be noted this correlation is not statistically significant.

Third, we performed multiple regressions comparing monthly precipitation to growth of each clone. For each clone except Clone 43, growth was significantly correlated with precipitation in at least one month. However, no two clones responded similarly to monthly precipitation. This suggests that, for these aspen clones, changes in monthly precipitation due to global warming could be more important than changes in total annual precipitation. For instance, if December precipitation increases and October precipitation decreases, growth Clone 29 will increase while growth of Clone 50 will decrease. This conclusion would hold even if total annual precipitation decreases. This is very interesting! A study should be conducted to further explore how *P.tremuloides* clones are responding to changes in monthly precipitation.

We could not address our second question due to lack of correlation between annual rainfall and growth (figure 4). Although this showed a lack of sensitivity of the clones to precipitation there is evidence that the clones do respond to annual precipitation differently. For example, Clone 29 showed a non-linear correlation that was not found in any of the other clones. This supports the above conclusion.

In our final question we asked if certain clones respond better than others to dry conditions. We compared three low precipitation years and found that Clone 29 grew significantly better; therefore there should not be a change in the dominance hierarchy: Clone 29 should continue to do well as soil moisture lessens due to increased evaporation. This does not suggest strong evidence of genetic variation, although genetic variation may be present, but it does suggest Clone 29 is the dominant clone. The results of the comparison with the four high years also indicated that future decreased moisture availability due to global warming will favor the continued dominance of Clone 29.

In the context of the final question we also asked if there were intraclonal variances. Surprisingly, different trees within a clone showed highly varied responses to precipitation levels. We expected trees to show a positive correlation, based on previous studies (Stocker, 1960 and Brix, 1962), however, no overall trend was found; in fact, some trees growth were negatively correlated with precipitation variables. We can provide no mechanistic explanation for these negative correlations.

Why is this important to the scientific community? Our results also show that three clones responded to precipitation in significant months; however, none of the clones responded significantly to summer months which are currently the focus of much investigation, indicating that growth may be more strongly correlated to other months. Currently there is a focus on annual precipitation to predict global climate change consequences. Our study shows no significant correlation between annual precipitation and growth, indicating that annual precipitation prediction models may not be the best way to predict consequences of global climate change. Monthly precipitation may be more relevant to predicting consequences of global climate change. Therefore, global climate change models may not be accurate without modeling the monthly distribution of precipitation change as a consequence of global warming.

LITERATURE CITED

Barnes, Burton V. 1966. The clonal growth habit of American aspens. Ecology 47(3): 439-447.

Brix, H. 1962. The effect of water stress on the rates of photosynthesis and respiration in tomato plant and loblolly pine seedlings. Physiologia Pl. 15, 10-20.

Clyne, Andrea, Jeff Firestone, and Andrea Pullo. 1998. Son of a Beech, the Moose are Back!: Effect of Glacial History on Plant Communities. Unpublished abstract, Dave Karowe's spring General Ecology class, UMBS.

Frahm, Anne M. 1995. Gender-specific physiology in trembling aspens, *Populus tremuloides*. University of Michigan Biological Station, Pellston, MI.

Gates, David M. 1993. Climate change and its Biological Consequences. Sinauer Associates, Sunderland, MA.

Gates, C.T. and Bonner, J. 1959. The response of the young tomato plant to a brief period of water shortage. IV. Effects of water stress on the ribonucleic acid metabolism of tomato leaves. Plant Physiology., Lancaster 34, 49-55

Geophysical Fluid Dynamics Laboratory (GFDL). 1998. National Oceanic & Atmospheric Administration. Princeton, N.J. [Online] Available: http://www.gfdl.gov/~tk/climate_dynamics/climate_impact_webpage.html

Graham, Samuel A. 1963. Aspens: Phoenix Trees of the Great Lakes Region. The University of Michigan Press, Ann Arbor, MI.

Roth, Sherry, Evan P. McDonald, and Richard L. Lindroth. 1997. Atmospheric CO_2 and soil water availability: consequences for tree-insect interactions. Canada Journal For. Res. 27:1281-1290.

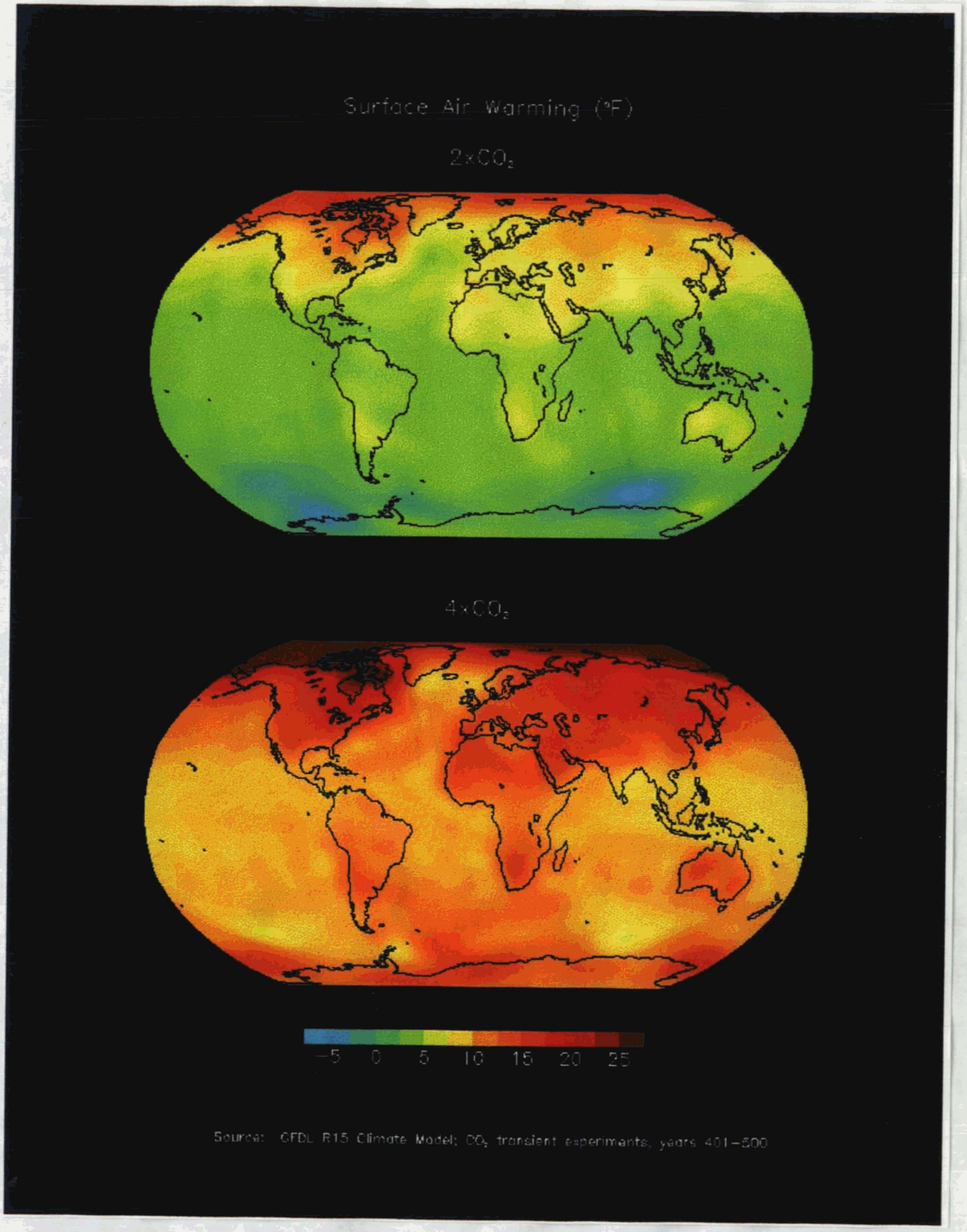
Schweingruber, Fritz H. 1989. Tree Rings: Basics and applications of dendrochronology. Kluwer Academic Publishers, Holland.

Shands, William E. 1987. The Greenhouse Effect, Climate Change, and U.S. Forests. The Conservation Foundation, Washington, D.C.

Slatyer, R.O. 1967. Plant-water Relationships. Academic Press, London and New York.

Stocker, O. 1960. Physiological and morphological changes in plants due to water deficiency. UNESCO Arid Zone Res. 15, 63-104

Wetherald, Richard T. 1991. Changes of temperature and hydrology caused by an increase of atmospheric carbon dioxide as predicted by general circulation models. Pages 1-17 in Wyman, Richard L. (ed)., Global Climate Change and Life on Earth. Chapman and Hall, Inc., New York, N.Y.



Surface Air Warming (°F)

$2 \times CO_2$

$4 \times CO_2$

Source: GFDL R15 Climate Model; CO_2 transient experiments, years 401−500

Fig. 1

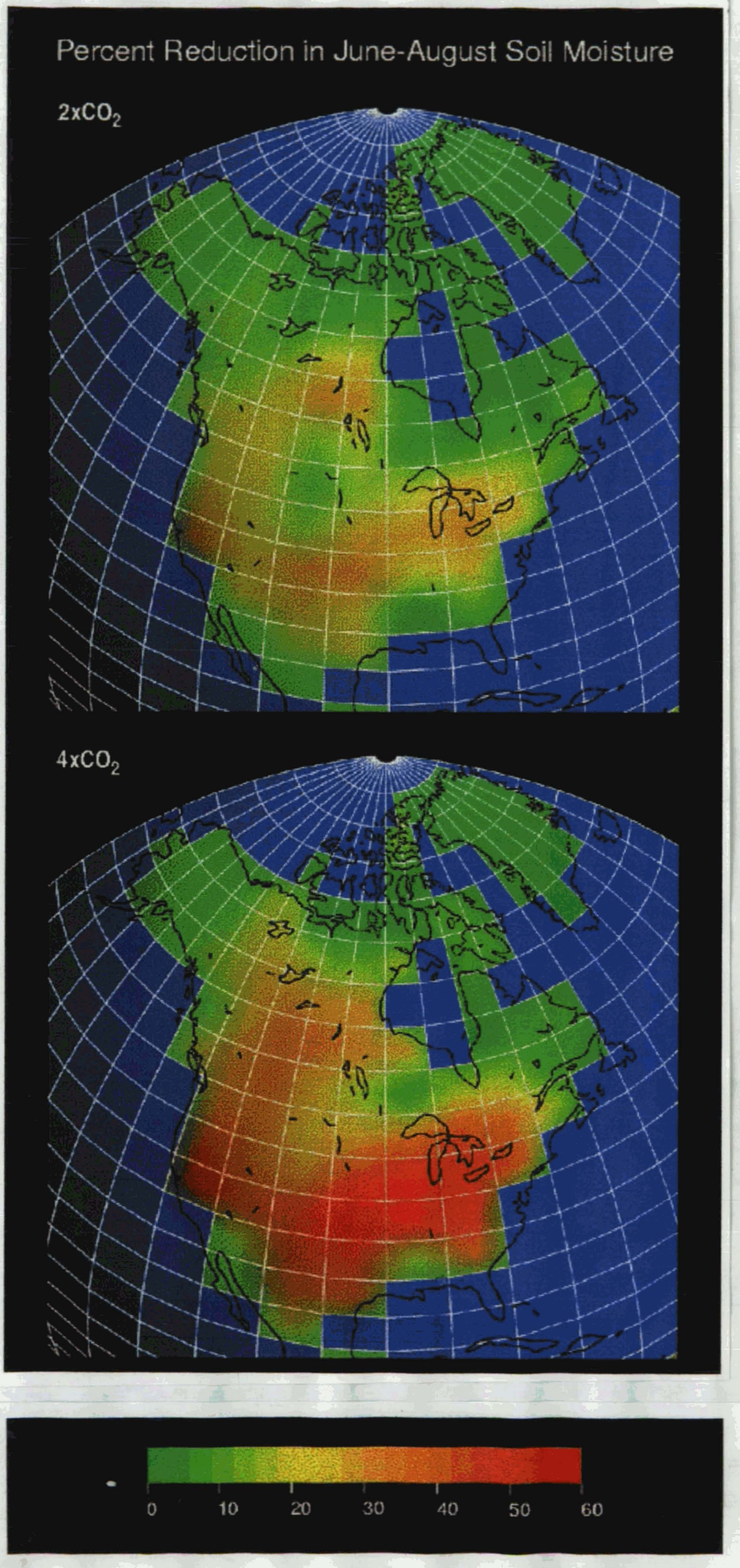

Percent Reduction in June-August Soil Moisture
$2xCO_2$
$4xCO_2$
0
10
20
30
40
50
60

Fig. 2

Pellston Plain research site (*P. tremuloides* clones marked in red)

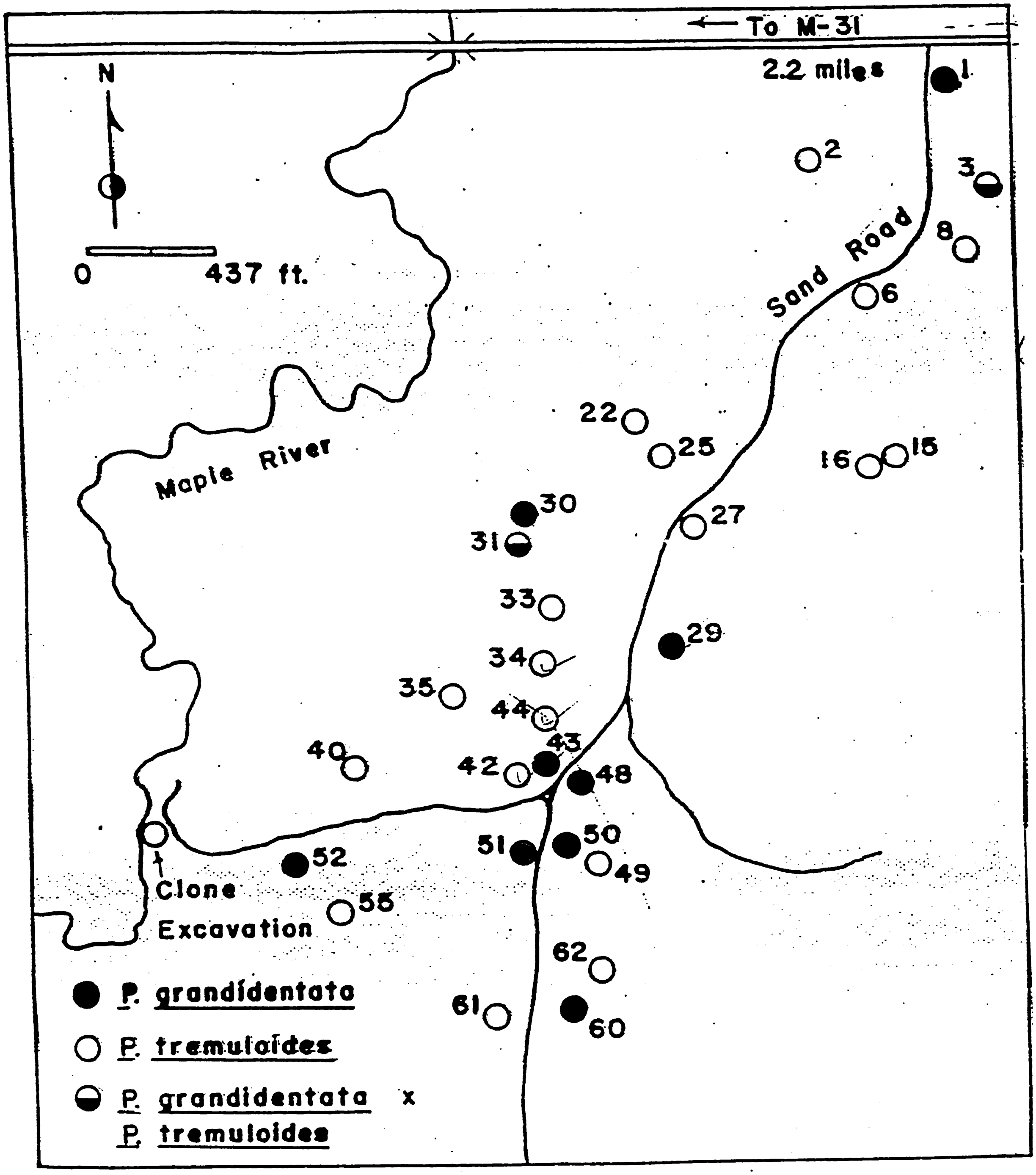
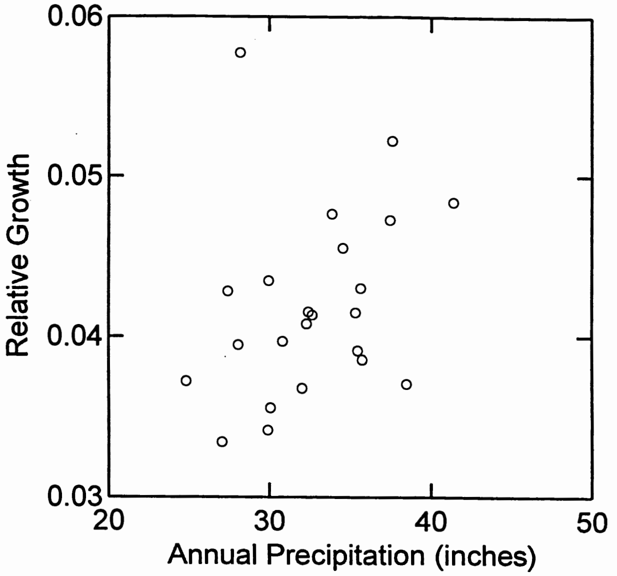


Fig. 3

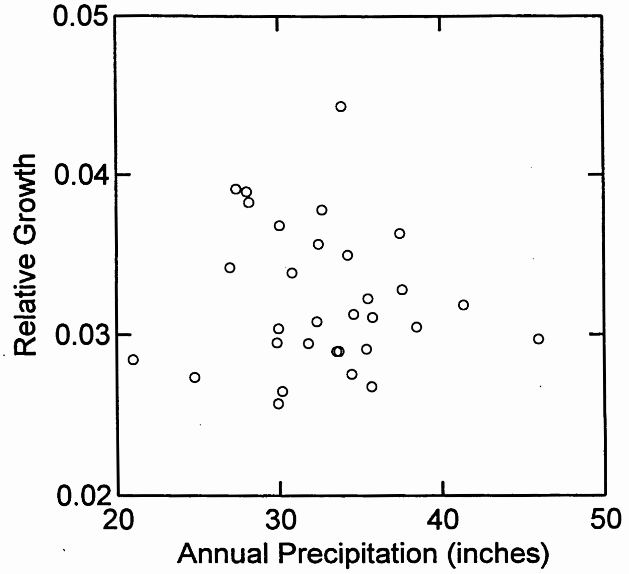
Clonal Responses to Annual Precipitation

Clone 29



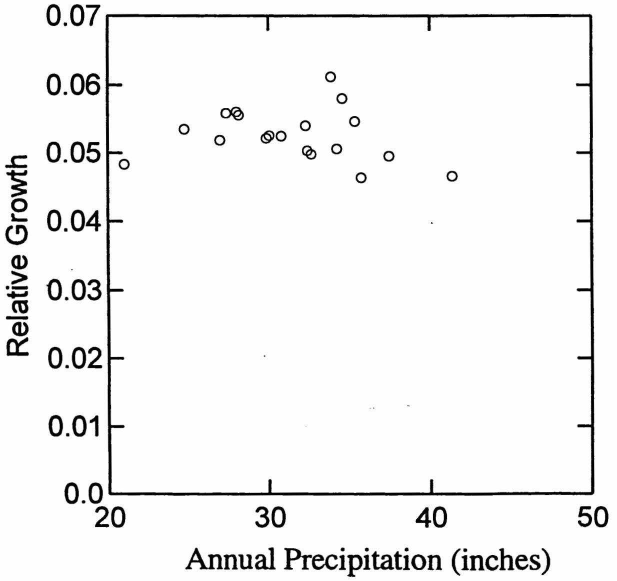
p = 0.116

Clone 43



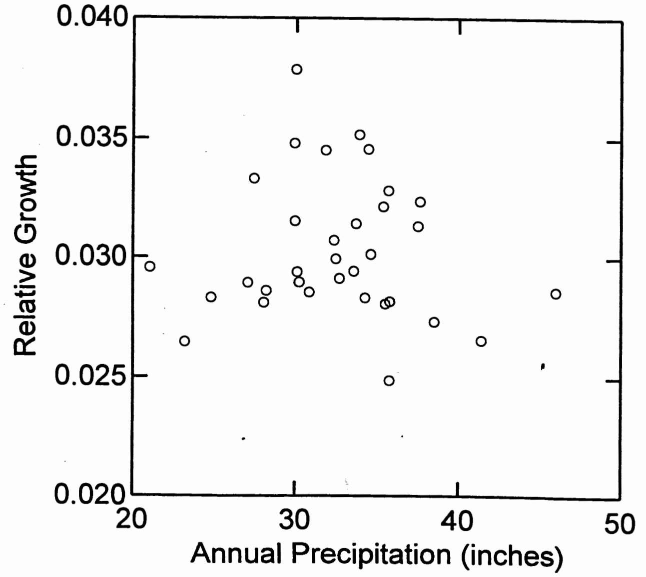
p=0.734

Clone 50



p = 0.434

Clone 51



p = 0.763

Fig. 4

Multiple Regression Analyses for Clone Response to Monthly Precipitation

Clone 29

```
--------------------------------------------------------------------------------
Dependent variable: MEANA
--------------------------------------------------------------------------------
                                        Standard             T
Parameter                 Estimate        Error          Statistic        P-Value
--------------------------------------------------------------------------------
CONSTANT                 0.0352384     0.00336585        10.4694          0.0000
OCT                   -0.000499985    0.000292767       -1.70779          0.1032
AUG                     0.00113868    0.000723348        1.57418          0.1311
DEC                     0.00219114     0.00101194        2.16528          0.0426
--------------------------------------------------------------------------------

                           Analysis of Variance
--------------------------------------------------------------------------------
Source             Sum of Squares     Df  Mean Square      F-Ratio       P-Value
--------------------------------------------------------------------------------
Model                 0.000215913      3 0.0000719709        2.48         0.0904
Residual              0.000579918     20 0.0000289959
--------------------------------------------------------------------------------
Total (Corr.)         0.000795831     23

R-squared = 27.1305 percent
R-squared (adjusted for d.f.) = 16.2001 percent
Standard Error of Est. = 0.00538479
Mean absolute error = 0.00374921
Durbin-Watson statistic = 1.68121
```

Clone 50

```
--------------------------------------------------------------------------------
Dependent variable: AVGRELGROW
--------------------------------------------------------------------------------
                                        Standard             T
Parameter                 Estimate        Error          Statistic        P-Value
--------------------------------------------------------------------------------
CONSTANT                 0.0523171      0.0105975        4.93675          0.0001
DEC                    -0.00591681     0.00285847       -2.06992          0.0540
JULY                   -0.00455164     0.00222541        -2.0453          0.0566
OCT                     0.00531361     0.00206543        2.57264          0.0198
--------------------------------------------------------------------------------

                           Analysis of Variance
--------------------------------------------------------------------------------
Source             Sum of Squares     Df  Mean Square      F-Ratio       P-Value
--------------------------------------------------------------------------------
Model                  0.00204575      3  0.000681916        3.59         0.0356
Residual               0.00323021     17  0.000190013
--------------------------------------------------------------------------------
Total (Corr.)          0.00527596     20

R-squared = 38.7749 percent
R-squared (adjusted for d.f.) = 27.9705 percent
Standard Error of Est. = 0.0137845
Mean absolute error = 0.00881574
Durbin-Watson statistic = 1.10893
```

Clone 51

```
--------------------------------------------------------------------------------
Dependent variable: RELMM
--------------------------------------------------------------------------------
                                        Standard             T
Parameter                 Estimate        Error          Statistic        P-Value
--------------------------------------------------------------------------------
CONSTANT                 0.0335369     0.00227949        14.7124          0.0000
DEC                    0.000606799    0.000373557        1.62438          0.1164
MAY                    0.000543256     0.00035312        1.53845          0.1360
APRIL                 -0.000902335    0.000397962       -2.26739          0.0319
FEB                    0.000959749    0.000498194        1.92646          0.0650
NOV                   -0.000940847    0.000371871       -2.53003          0.0178
SEPT                  -0.000562664    0.000239353       -2.35078          0.0266
--------------------------------------------------------------------------------

                           Analysis of Variance
--------------------------------------------------------------------------------
Source             Sum of Squares     Df  Mean Square      F-Ratio       P-Value
--------------------------------------------------------------------------------
Model                 0.000122933      6 0.0000204888        3.66         0.0091
Residual              0.000145506     260.00000559638
--------------------------------------------------------------------------------
Total (Corr.)         0.000268438     32

R-squared = 45.7954 percent
R-squared (adjusted for d.f.) = 33.2867 percent
Standard Error of Est. = 0.00236567
Mean absolute error = 0.00176856
Durbin-Watson statistic = 2.43497
```

Fig. 5

Clone 43

```
ltiple Regression Analysis
------------------------------------------------------------------------------
ependent variable: MEAN
------------------------------------------------------------------------------
                                        Standard          T
Parameter               Estimate          Error        Statistic       P-Value
------------------------------------------------------------------------------
CONSTANT               0.0249776      0.00272186        9.17666         0.0000
FEB                    0.0010904     0.000815507        1.33708         0.1906
AUG                  0.000647654     0.000437886        1.47905         0.1489
SEPT                -0.000551466     0.000345836       -1.59459         0.1206
JAN                  -0.00146349     0.000731463       -2.00076         0.0540
------------------------------------------------------------------------------

                           Analysis of Variance
------------------------------------------------------------------------------
Source             Sum of Squares     Df  Mean Square     F-Ratio      P-Value
------------------------------------------------------------------------------
Model                 0.000118666      4 0.0000296665        1.82       0.1497
Residual              0.000522331     32 0.0000163228
------------------------------------------------------------------------------
Total (Corr.)         0.000640997     36

R-squared = 18.5127 percent
R-squared (adjusted for d.f.) = 8.32679 percent
Standard Error of Est. = 0.00404015
Mean absolute error = 0.00300422
Durbin-Watson statistic = 0.945969
```

Summary of significant correlations of clonal growth with individual months

Clone	Months
29	Dec. (p=0.043)
50	Oct. (p=0.198)
51	Apr. (p=0.032)
	Nov. (p=0.018)
	Sept. (p=0.023)

Individual ramet growth responses to annual and monthly precipitation

	Clone 29	Clone 43	Clone 50	Clone 51
	relative growth	relative growth	relative growth	relative growth
Precipitation				
Annual	(+) 4a, 9a, 12a, 15a			(+) 3a
		(-) 1a	(-) 10a	
January	(+) 4a		(+) 11a	(+) 7a
		(-) 2a, 9a		(-) 12a
February			(+) 15a	(+) 3a, 14a, mean
	(-) 11a			
March		(+) 13a	(+) 7a, 8a	
April				
		(-) 15a	(-) 4a, 9a, 12a, mean	(-) 8a
May				
		(-) 9a	(-) 10a	
June	(+) 3a	(+) 5a, 15a		
		(-) 13a		
July	(+) 15a			
	(-) 3a	(-) 1a, 4a, mean	(-) 4a, 10a, 12a	
August			(+) 12a, mean	
			(-) 10a	(-) 12a, 14a
September	(+) 15a		(+) 2a	
			(-) 9a	(-) 14a
October	(+) 1a		(+) 13a	
				(-) 14a
November		(+) 7a	(+) 2a	
		(-) 9a, 14a		(-) 7a, mean
December	(+) 1a, 11a		(+) 1a, 13a	(+) 1a
		(-) 9a, 14a	(-) 9a, 12a	

Legend:

(+) or (-) indicates sign of r
Numbers followed by "a" indicate numbers of ramets which show significant correlation with monthly precipitation

Table 1

Mean absolute growth for clones in high and low precipitation years

	low	precipitation		high	precipitation		
year	**1966**	**1989**	**1992**	**1972**	**1974**	**1978**	**1984**
precipitation	23.23	27.44	32.06	46.02	37.65	38.52	37.52
	p=.038	p<.0005	p=.02	p<.0005	p=.002	p<.0005	p<.0005
clone 29							
mean	.024533	.02726725	.027	.029154	.032571	.025	.030429
s.d	.011457	.01171	.016149	.013789	.013472	.010713	.010761
	(n=6)	(n=15)	(n=15)	(n=13)	(n=14)	(n=14)	(n=14)
	a	a	a	a	a	a	a
clone 43							
mean	.019308	.019308	.021357	.022429	.024143	.023	.025357
s.d.	.00791	.007376	.008767	.008864	.007794	.008345	.008345
	(n=14)	(n=15)	(n=15)	(n=14)	(n=14)	(n=12)	(n=14)
	a	a	a	a	b	ab	a
clone 50							
mean	N.A.	.019933	.016567	.01275	.01675	.018417	.016929
s.d	N.A.	.007045	.006992	.005497	.009864	.008207	.007478
		(n=15)	(n=15)	(n=8)	(n=12)	(n=12)	(n=14)
	b	b	b	b	bc	bc	b
clone 51							
mean	.014286	.016857	.0155	.014429	.016429	.0135	.016143
s.d	.00768	.005789	.00588	.002901	.003756	.002876	.005157
	(n=14)	(n=14)	(n=14)	(n=14)	(n=14)	(n=14)	(n=14)
	-	b	b	b	c	c	b

Legend: clones with the same letter are not significantly different at $p<0.05$ for each year.

Table 2.