Final Project Report

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Abstract

The invasive thistle *Carduus nutans* has been a management concern for landowners and governments alike, with dispersal in this plant playing an important role in its spread. Given that the terminal velocity of *C. nutans* seeds strongly influences dispersal distance, we seek to beter understand how both pappus shape and treatment of the parent plant affect seed terminal velocity. Our analyses show that the width of the seed pappus was the most important factor in determining seed terminal velocity and that the two were negatively correlated, with higher pappus width generally giving rise to a lower terminal velocity. Warming and mowing treatments on the parent plants had significant effects on the pappus width, with warmed and mowed plants having a much smaller pappus width. Regarding the effects of the treatments on seed terminal velocity, early mowing increased terminal velocity, while warming decreased terminal velocity; no significant effect was observed for late mowed plants compared to control plants. Given that mowing was shown to increase pappus width and that increased pappus width was shown to reduce terminal velocity, it is surprising that plants experiencing the early mowing treatment had higher seed terminal velocity. Such a contridiction merits further investigation of additional factors, such as mass, that may affect seed terminal velocity.

Introduction and Data

As the world has become significantly more interconnected, the increased movement of people across the world has also facilitated an increase in the spread of species outside of their native ranges. When species that are introduced outside of their native range become invasive, they can have a detrimental impact on local biodiversity, quantity and quality of valuable ecosystem services, and other aspects of the local ecosystem. Because of this, the study of invasive species has been a large part of the ecology literature in recent decades, ranging from theoretical models of how they spread to investigating possible management practices that keep them at bay.

One particular invasive species that has greatly expanded its range due to human activity is *Carduus nutans*, also known as "musk thistle" or "nodding thistle". This thistle is native to Europe and Central Asia, but has expanded its range into North America, Australia, and New Zealand, among other parts of the world[1]. Within the U.S., this thistle has been reported in all U.S. states except for Alaska, Florida, Hawaii, Maine, and Vermont[2]; the thistle may even be present in these states, but has not yet been reported. It is also been reported all Canadian provinces except Nunavut, Northwest Territories, and Yukon Territories[2].

C. nutans is considered to be a noxious weed in many U.S. states for several reasons. Because it can occur in very large numbers and grow to be quite large, this thistle may form dense and often impenetrable stands. The plant is also covered in numerous large spines, making it painful when touched as well as unpalatable to grazing animals. The adverse impacts of this weed on grazing can also lead to substantial economic losses.

Another reason why there is concern over *C. nutans* is because it has a high potential to spread locally when introduced. This thistle is wind dispersed and seeds have a large pappus, or a feathery and lightweight modified calyx, on the seeds that allows them to be transported great distances. Models have been proposed to model such wind-driven seed dispersal[3], and such models have been applied to *C. nutans*[4], showing significant potential for long-range dispersal events. While there are abiotic and biotic factors that affect how far a seed like those in *C. nutans* can be dispersed, a noteworthy predictor of dispersal distance is seed terminal velocity. For seeds, a higher terminal velocity generally means a decreased dispersal distance; this is because a higher terminal velocity means the seed falls faster and thus spends less time in the air, which means less of an opportunity for wind to carry it further from its source.

However, it is not entirely clear what affects terminal velocity in *C. nutans* seeds, though the most obvious candidates would be physical properties of the seed such as shape and mass. In general, seeds with a larger area perpendicular to the direction of motion will have higher drag and a lower terminal velocity. Seeds with a higher mass will have a higher downward force (mg) from gravity and thus a higher air resistance force that must equal it to achieve terminal velocity, which leads to a higher terminal velocity since said resistance force is proportional to that velocity. However, the physical properties of the seed may be affected by the morphology and physiology of the parent plant; abiotic and biotic factors can affect the parent plant in such a way that may ultimately influence the terminal velocity of its seeds.

Given that there may be a link between abiotic influences on *C. nutans* and the terminal velocity of its seeds, we wish to investigate whether certain treatments applied to the plant before it flowers have any effect on seed dispersal capabilities. Any treatment effects that can reduce the dispersal capability of these thistles may then be used to inform management decisions. By using mowing treatments as well as warming treatments (and combinations of the two), we will examine the effects of said treatments on seed terminal velocity and thus on dispersal capability.

The data used to assess the effects of mowing and warming on seed terminal velocity were collected during a field experiment that involved applying these treatments to parent plants and collecting their flower heads aftey they had set seed. The experimental setup involves ten blocks, with each block containing two plots: one plot with a warming treatment and one without. Within each plot there are three positions: one with an early mowing treatment, one with a late mowing treatment, and one with no mowing at all. Overall, this yields six unique combinations of warming and mowing, with 10 replicates for each combination. Ten seeds were planted at each position, and one flower head was harvested from all individuals that survived to harvest date. Seeds were collected from individual flower heads and their terminal velocities were determined by timing the amount of time it took them to afll through a 1.25-m drop chamber. For each seed, these drop tests were repeated until two consecutive drop times were recorded within 0.1 seconds of each other.

Using the data from the experiment described above, we seek answers to three research questions of interest:

1. Is seed terminal velocity predicted by the shape of the seed pappus?
2. To what extent do warming and mowing treatments change seed terminal velocity?
3. Can changes in terminal velocity by treatment be explained by changes in seed shape parameters?

Research Question 1

Before any models were fit to the data, we first examined correlations between the various seed physical properties. The `pairs` plot for terminal velocity and the various physical properties is shown below:

Linear correlations between the variables can also be shown in a heatmap of the correlation matrix:

Between both of these plots, it is clear that multicollinearity will be an issue since several of the variables are highly correlated with each other (e.g. `SeedWidth` and `SeedAngle`, `SeedWidth` and `SeedArea`, etc.).

Our first model used the terminal veocity `TV` as a response and each of the physical properties as predictors. The resulting coefficients and their significance are listed below:

	Estimate	Std. Error	t value	Pr(>|t|)	VIF	Significance
(Intercept)	1.7939	0.2872	6.2465	0		***

	Estimate	Std. Error	t value	Pr(>|t|)	VIF	Significance
SeedWidth	-0.0902	0.0294	-3.0629	0.0024	231.7271	**
SeedLength	0.2323	0.1394	1.6664	0.0965	1672.8695	.
SeedArea	-0.0012	0.0021	-0.5918	0.5544	918.6289	
SeedAngle	-0.2099	0.4397	-0.4774	0.6334	291.9196	
SeedHeight	-0.2336	0.1536	-1.5214	0.129	2709.2157	
SeedVol	4e-04	2e-04	2.2275	0.0265	124.7234	*

It is clear that this model is a poor fit for two main reasons. First, many of the terms are not significant to $\alpha = 0.05$ and add no significant additional predictive power to the model. Second, the VIF for all of the coefficients is quite high, as was predicted.

Given that some of these variables must be removed to improve the fit of the model, we then performed variable selection on the full model to reduce clutter. The first method of selection was backwards selection from the full model; this involved removing subsequent variables based on their p-value; the variable with the highest p-value was removed, the resulting model examined, and the process repeated until all predictors were significant. The second method of selection involved backwards selection from the full model using AIC, where terms were removed until the AIC of the model was minimised. The third mehtod of selection started from the full model and used `step` selection in both directions, while the fourth method started from the null model and added terms; again, in both cases, the selection continued until the AIC of the model was minimised.

The results from the model selection can be seen below, along with the VIF for each term as well as both the AIC and R^2 for each resulting model. All coefficients are significant to $\alpha < 0.001$.

	Method 1	Method 2	Method 3	Method 4	Method 1,2,3 VIF	Method 4 VIF
(Intercept)	1.6698759	1.6698759	1.6698759	1.6694531		
SeedWidth	-0.1027270	-0.1027270	-0.1027270	-0.0865305	37.38156	29.50804
SeedLength	0.1536113	0.1536113	0.1536113		69.98712	
SeedArea				-0.1470827		29.50804
SeedAngle						
SeedHeight	-0.1470827	-0.1470827	-0.1470827		72.02489	
SeedVol	0.0002749	0.0002749	0.0002749		14.85025	
AIC	-1293.6000000	-1293.6000000	-1293.6000000	-1288.4000000		
R^2	0.3921194	0.3921194	0.3921194	0.3803212		

As we can see in the table, the first three selection methods produced the exact same result, while the fourth method produced a result with fewer terms. While the model derived from the first three methods has a higher R^2 and lower AIC than the model derived from the fourth method, it suffers greatly from high VIC. Because the VIF on the second model is much lower that that of the first and the difference in R^2 is very small, we will proceed with the second model, effectively trading a small increase in the amount of unexplained variance for a large decrease in multicollinearity.

However, we still see a rather high VIF for the `SeedWidth` and `SeedArea` terms. While the `SeedArea` term may be inflating estimates when added to `SeedWidth`, a partial F-test confirms that its addition is statistically significant ($F = 32.43$, $p < 0.001$). Since `SeedArea` is proportional to the square of `SeedWidth`, we can simply express it as such in a polynomial regression instead of using a separate `SeedArea` variable for it.

Comparing this to a single-term model where VIF is not an issue, we see that a model with only `SeedWidth` is not as good of a fit, with an R^2 of 0.3274 compared to 0.3804 for the quadratic model. This is also clear when plotting the models against the data, as can be see below:

We can also compare the distribution of residuals between the two models to check their validity. As can be

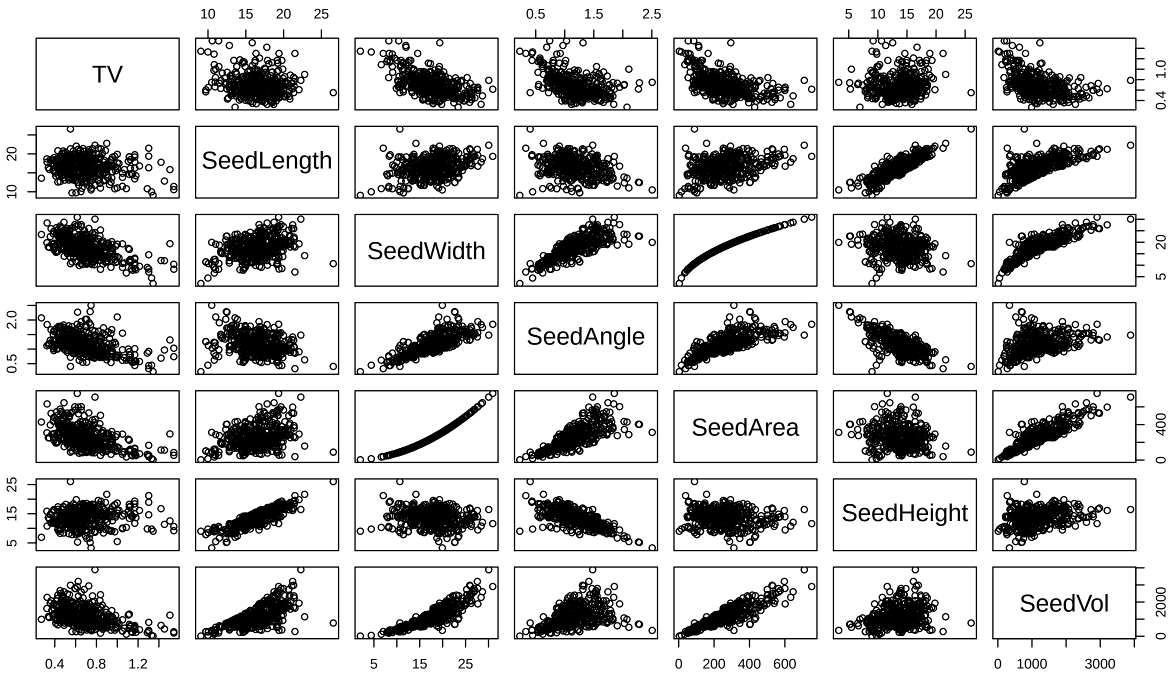


Figure 1: Plot of relationships between variables considered in this analysis.

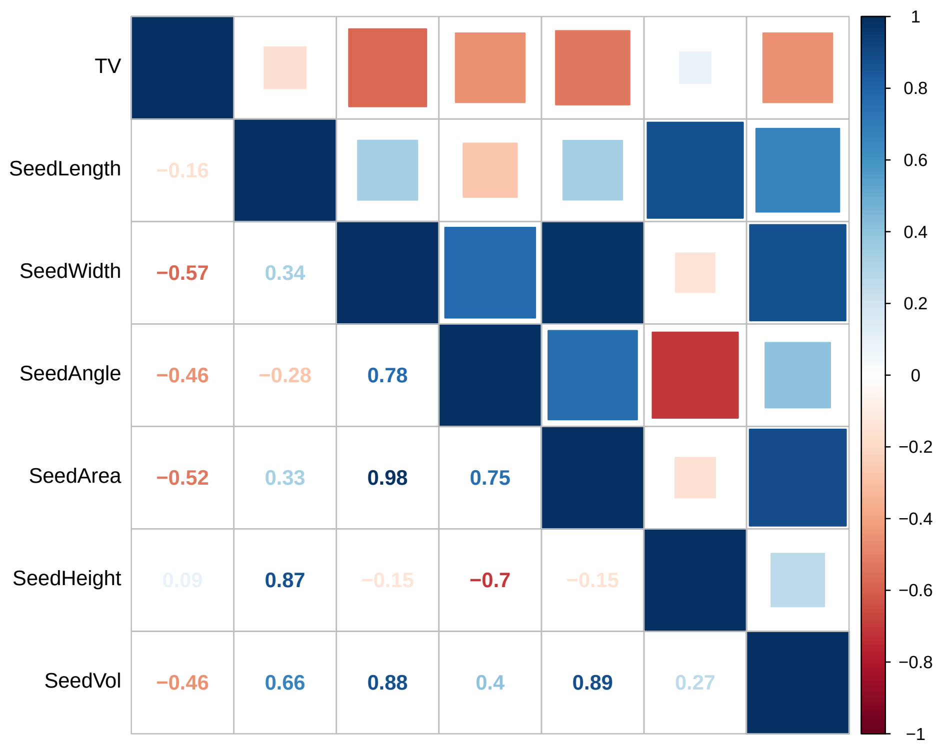


Figure 2: Correlations between variables considered in this analysis.

seen below, the residuals are approximately normally-distributed for both models, with a bit of deviation from normality at the tails of the distribution.

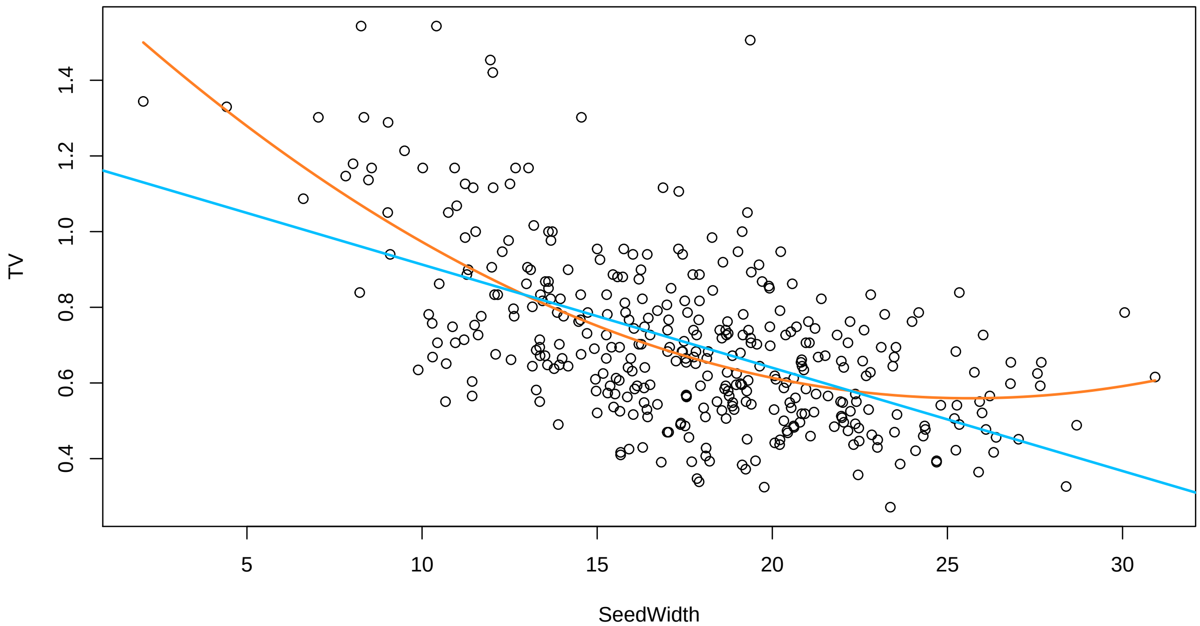


Figure 3: Plot of seed terminal velocity as a function of seed width. The two models are also plotted: the quadratic model (orange) and the linear model (blue).

However, there are clearly differences regarding patterns of distribution in the residuals. For the model with only `SeedWidth`, there appears to be some curvature in the distribution of residuals, suggesting that an invalid model has been fit to the data. However, in the model with both linear and quadratic `SeedWidth` terms, the curved pattern in the residuals disappears, suggesting that this model is more valid.

Research Question 2

Not only are we interested in predicting seed terminal velocity based on the physical properties of the seed, but we are also interested in quantifying the extent to which two environmental variables, warming and mowing, affect seed terminal velocity. Figure 7 shows variation in termnal velocity across all six treatments. Using this plot, we can generate a preliminary hypothesis that warming increases terminal velocity, while mowing decreases it. The following analyses will determine whether such differences are statistically significant. Figure 7 also shows that we have less data for late mowed plants, as many of them died.

Because we are fitting a continutous response variable to categorical predictor variables, we will use an ANOVA model to characterize changes in terminal velocity by treatmnet.We log-transformed terminal velocity to compensate for skewed right distribution of the terminal velocity data and significant deviations from error normality, as seen in Figure 8.

We used two methods to identify the most appropriate model fit for the log-transformed terminal velocity data. First, we fit the following four models:

- 'Mowing Only': $TerminalVelcotiy = \beta_0 + \beta_1 Mow$

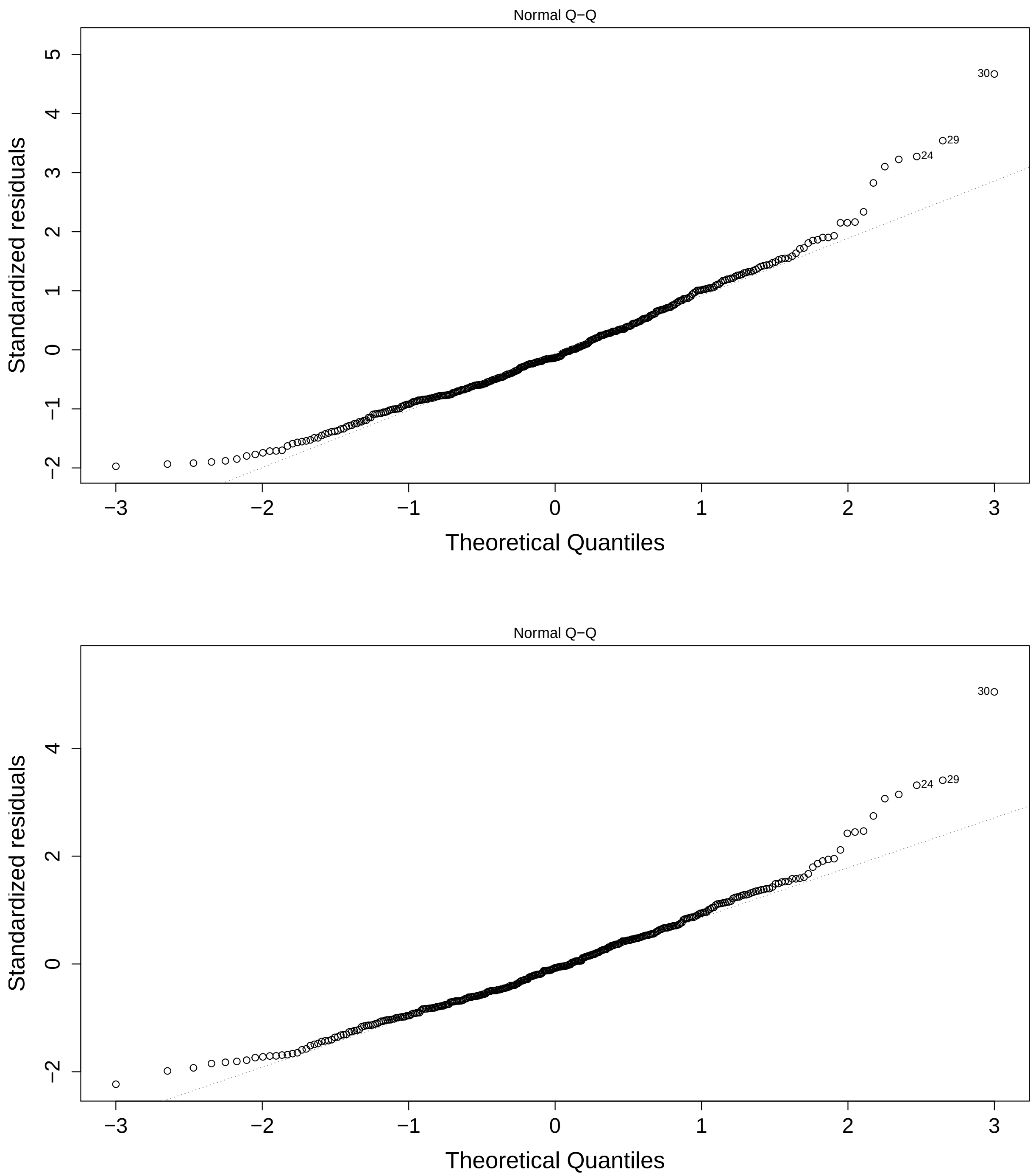
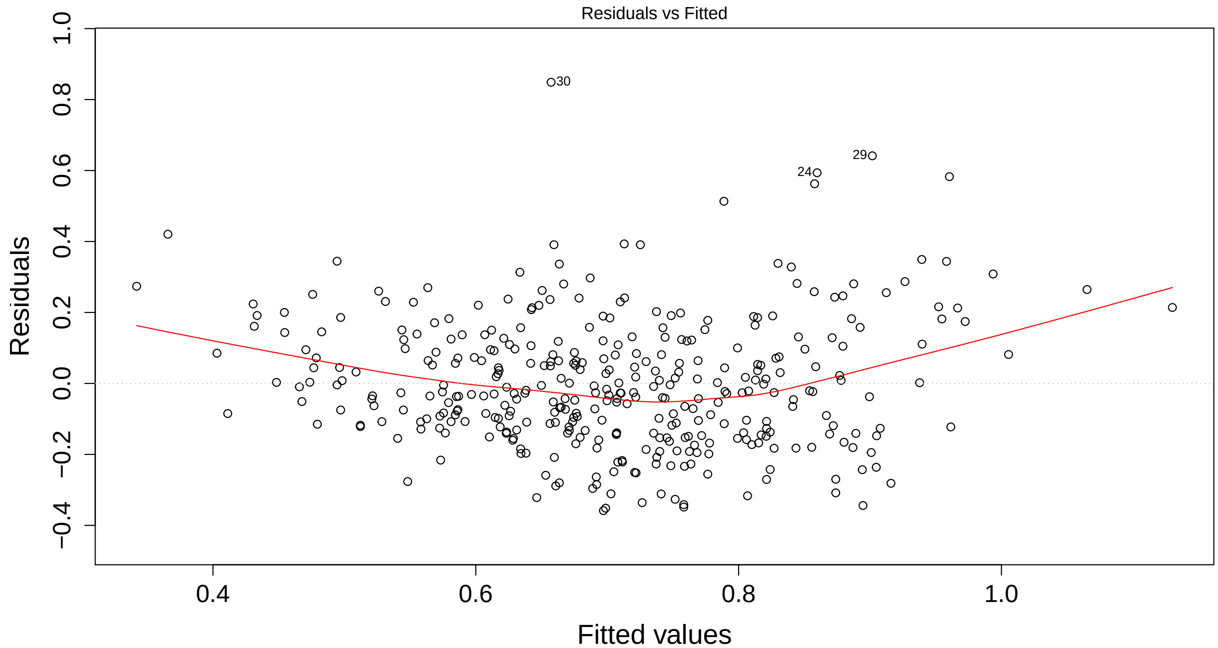


Figure 4: Q-Q Plots comparing normality of the residuals in the linear model (left) and quadratic model (right).



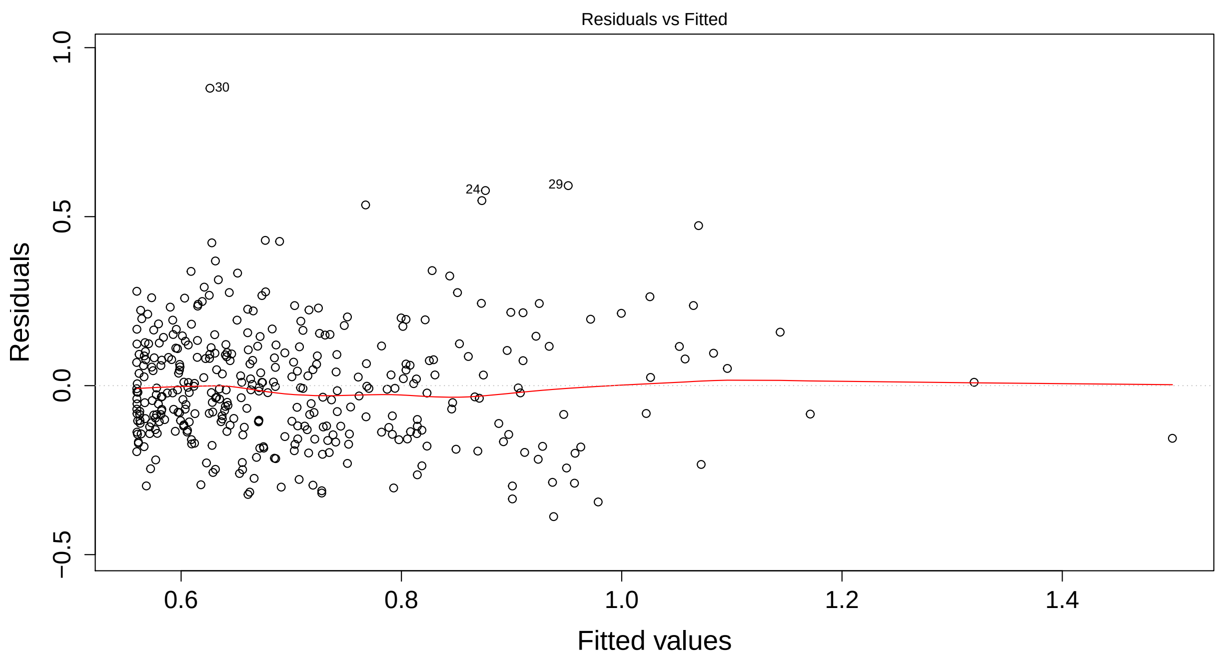


Figure 5: Comparison of residual distributions as a function of fitted values in the linear model (left) and quadratic model (right).

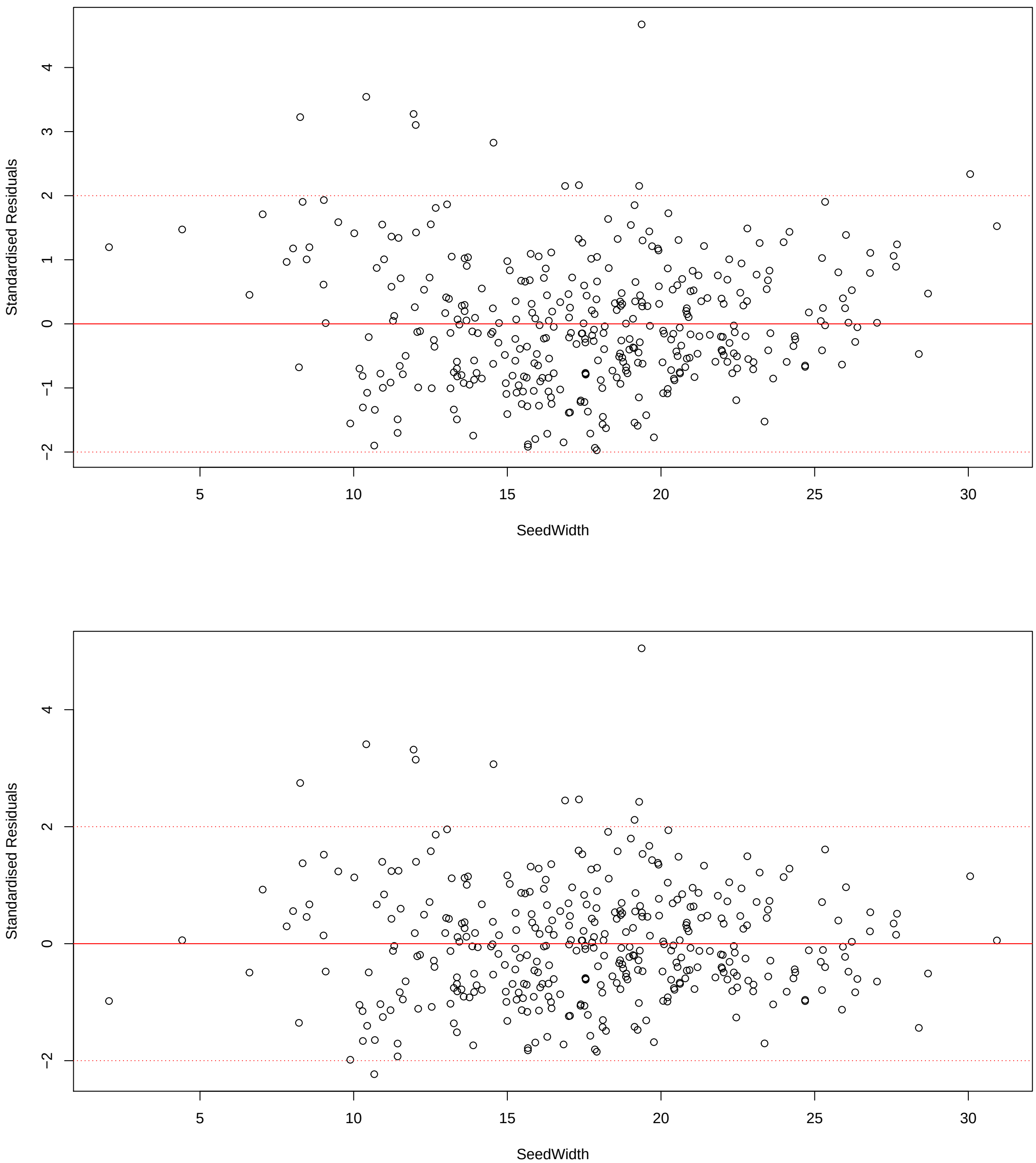


Figure 6: Comparison of standardised residual distributions as a function of observed values in the linear model (left) and quadratic model (right).

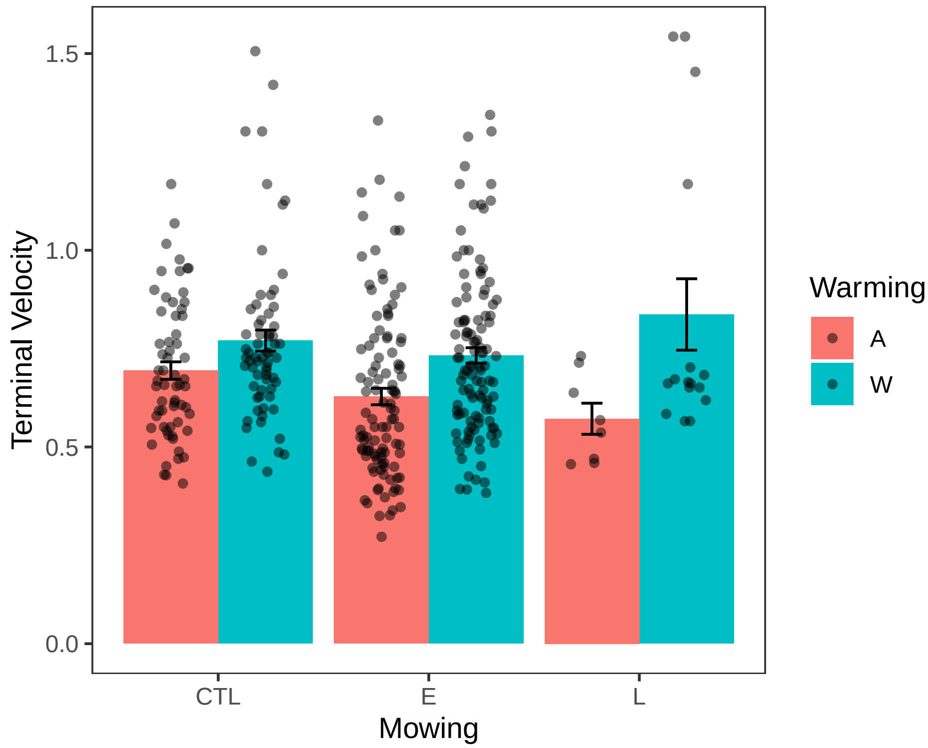


Figure 7: Terminal velocity for plants grown under warming and mowing treatments. Height of bar shows group mean, and error bars show one standard error. Actual data shown with black dots.

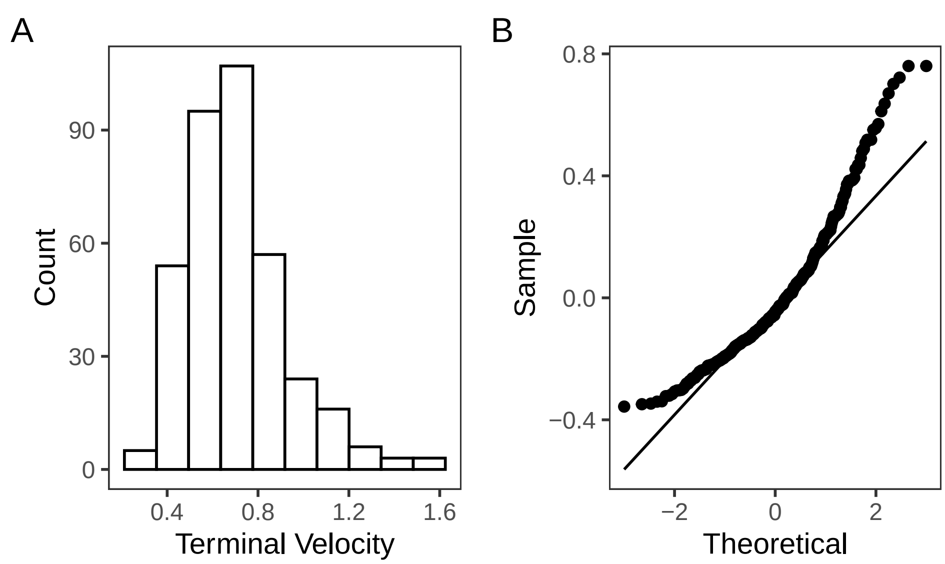


Figure 8: Justification for transofmraiton of terminal velocity. Histogram of terminal velocity (A) and Normal Q-Q plot of linear model with both warming and mowing predictors (B).

- ‘Warming Only‘: $TerminalVelocity = \beta_0 + \beta_1 Warm$
- ‘Warming and Mowing‘: $TerminalVelocity = \beta_0 + \beta_1 Mow + \beta_2 Warm$
- ‘Interaction‘: $TerminalVelocity = \beta_0 + \beta_1 Mow + \beta_2 Warm + \beta_3 Warm \cdot Mow$

We used model p-values for the `Mowing Only` and `Warming Only` models to establish which provided a better fit for the data. Then, with the better fitting model as a base, we performed a partial F-test to identify whether additional variables significantly improved model fit. Second, to validate the results of the partial F-test, we evaluated both the AIC and BIC for each model.

Here, the `Warming Only` model has a p-value of `0` whereas the `Mowing Only` model has a p-value of `0.0248`. Therefore, we use the `Warming Only` model as the base model in our partial F-test. Results, shown in Table 3, suggest that the `Warming and Mowing` model is the best fit for the data.

Table 3: Results of partial F-test comparing three models for predicting terminal velocity.

Model	P.Value
`Warming Only`	
`Warming and Mowing`	0.0217
`Interaction`	0.2134

Like the partial F-test, both AIC and BIC support the `Warming and Mowing` model (Table 4). Thus, we conclude that $TerminalVelocity = \beta_0 + \beta_1 Mowing + \beta_2 Warming$ is the best model fit for the log-transformed terminal velocity data.

Table 4: AIC and BIC values for each model.

Model	AIC	BIC
`Mowing Only`	162.1546	169.1052
`Warming Only`	162.1546	169.1100
`Warming and Mowing`	138.4409	147.1292
`Interaction`	139.3011	151.4648

The residuals for the `Warming and Mowing` model are shown in Figure 9. The residuals show approximately random distribution, and though there are a few points with high leverage, they do are not high includence accroding to Cook’s distance. Lastly, we can see that our log-transformation significantly improved the normality of the errors, as shown in the Normal Q-Q plot.

Model results are shown in Table 5 and treatment level predictions are shown in Figure 10. From these results, we conclude that early mowing significnatly decreases terminal velocity, whereas warming increases terminal velocity.

Table 5: Estimated coefficients and p-values for `Warming and Mowing` model. 95% confidence interval shown in parenthesis.

	Estimate	Pr(>|t|)
(Intercept)	-0.42 (-0.48, -0.36)	0
MowE	-0.09 (-0.15, -0.03)	0.01
MowL	-0.04 (-0.17, 0.09)	0.56
WarmingW	0.16 (0.1, 0.21)	0

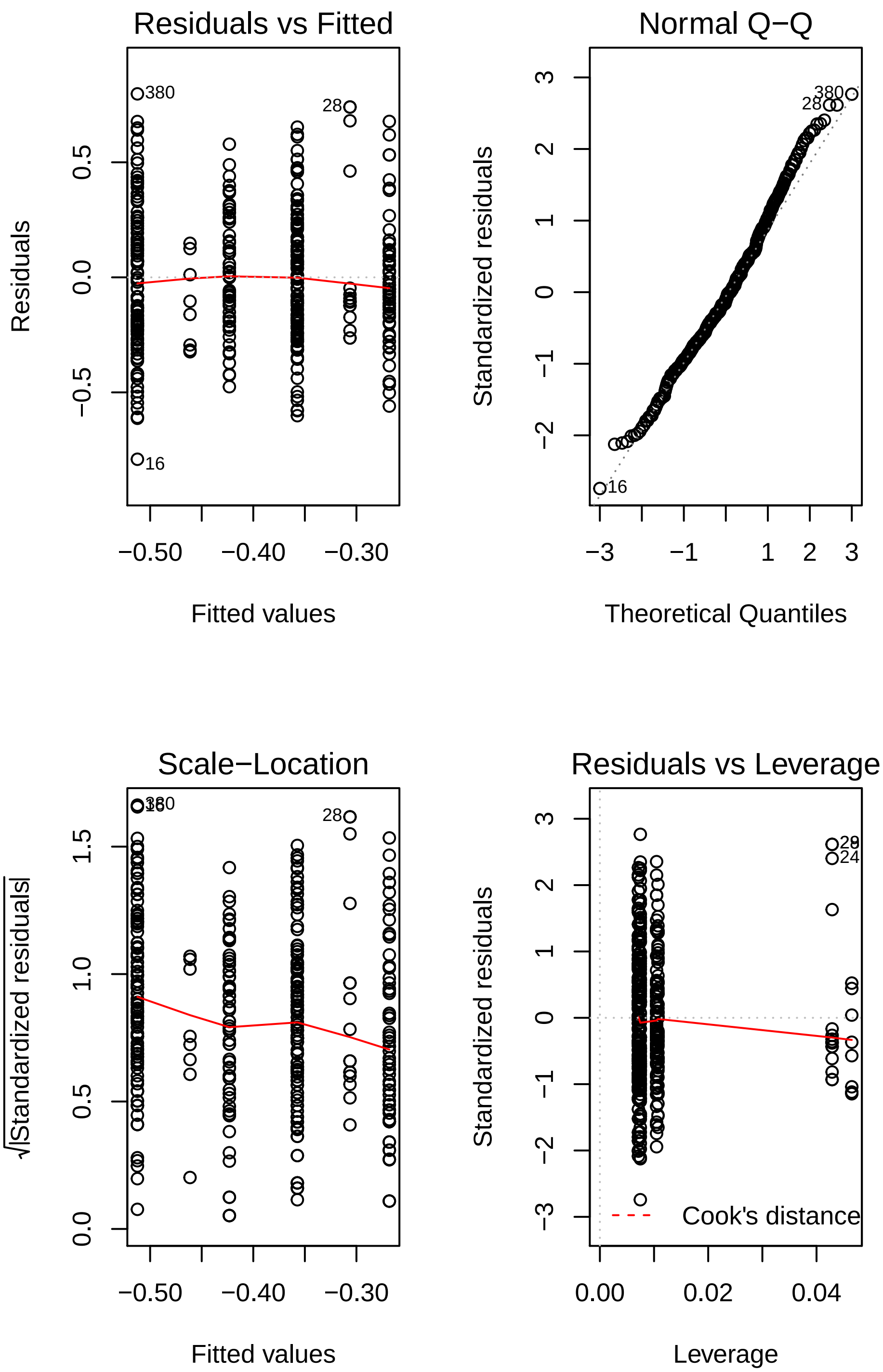


Figure 9: Diagnostic plots for `Warming and Mowing` model.

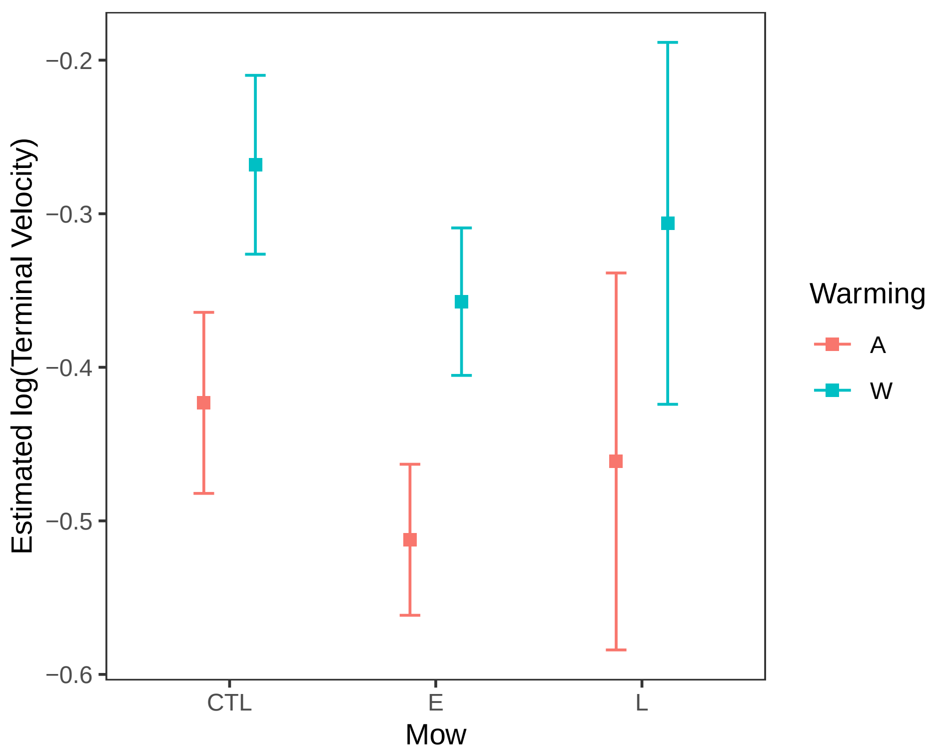


Figure 10: Results of best fitting ANOVA model, which included both warming and mowing as predictors. Square dots show mean predicted value and error bars show 95% confidence intervals.

Research Question 3

Next, we will explore the extent to which the results of Research Question 2, or the changes in terminal velocity by treatment, can be explained by changes in seed width. We are investigating seed width specifically because the results of Research Question 1 show that seed width is a good predictor of terminal velocity. Figure 11 shows the variation in seed width across treatments.

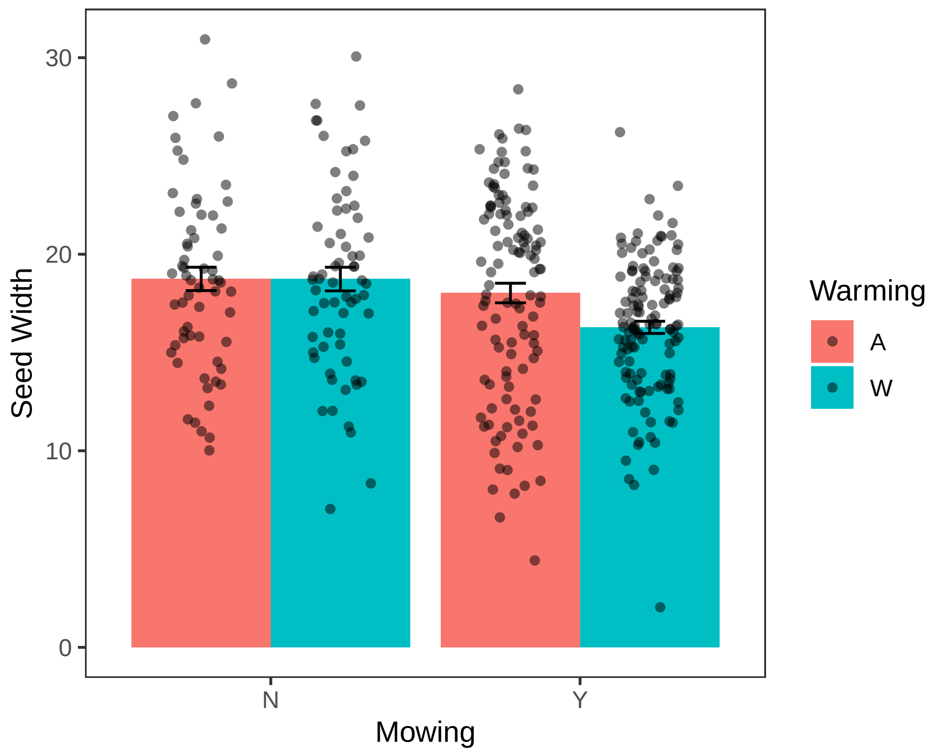


Figure 11: Seed width by warming and mowing treatments. Height of bar shows group mean, and error bars show one standard error. Actual data shown with black dots.

Our data fitting methods are similar to those of Research Question 2. We use partial F-tests and AIC/BIC analyses for model selection, but did not transform our response variable. First, we analyze the fit of the four basic models - mowing only, warming only, warming and mowing, and interaction - to identify which model is the best fit.

Here, the `Warming Only` model has a p-value of `0.0152` whereas the `Mowing Only` model has a p-value of `0.0031`. Therefore, we use the `Mowing Only` model as the base model in our partial F-test. Results suggest that the `Warming and Mowing` model is again the best fit for the data (Table 6.

Table 6: Results of partial F-test for models predicting seed width by treatment.

Model	P.Value
`Mowing Only`	
`Warming and Mowing`	0.0198
`Interaction`	0.2272

Again, we use AIC and BIC model selection criteria to validate these results. Table 7 shows similar results to those in Research Question 2, suggesting that the `Warming and Mowing` model is the best fit.

Table 7: AIC and BIC values for each of the four models predicting seed width.

Model	AIC	BIC
`Mowing Only`	2185.078	2192.028
`Warming Only`	2188.787	2194.000
`Warming and Mowing`	2181.592	2190.280
`Interaction`	2182.579	2194.743

Thus, both the partial F-test and the AIC/BIC values support the `Warming and Mowing` model, whose model diagnostic plots are shown in Figure 12. These residuals suggest the errors are approximately normally distributed. Again, there may be a few leverage points, though they do not have high influence.

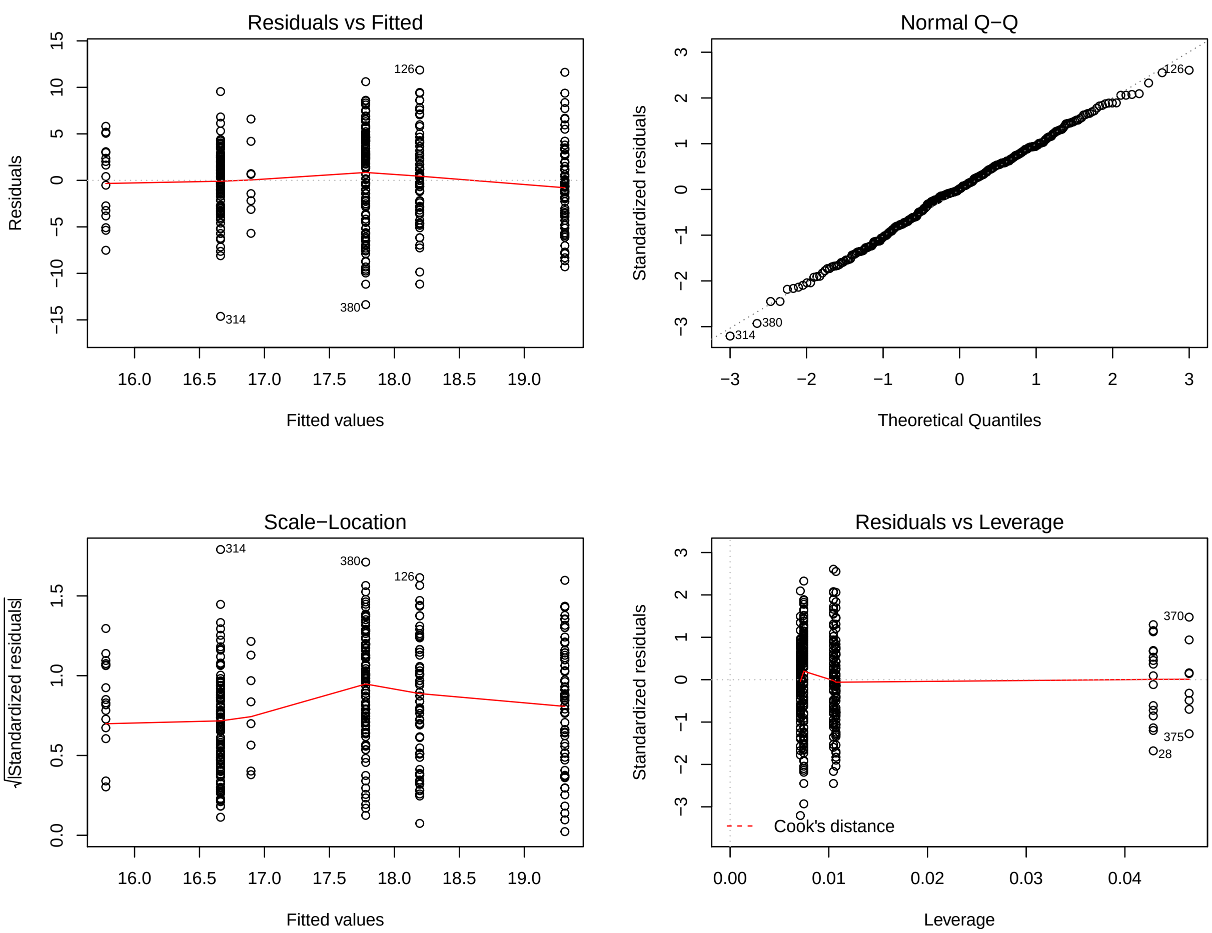


Figure 12: Diagnostic plots for predicting seed width using `Warming and Mowing` model.

Table 8 shows the results of the `Warming and Mowing` model for predicting seed width. These results suggest that both early mowing, late mowing, and warming signficantly decrease seed width.

Table 8: Results of `Warming and Mowing` model for predicting seed width. Coefficient estiamtes, 95% confidence intervals and p-values are shown.

	Estimate	Pr(>|t|)
(Intercept)	19.31 (18.38, 20.24)	0
MowE	-1.53 (-2.54, -0.53)	0
MowL	-2.42 (-4.42, -0.41)	0.02
WarmingW	-1.12 (-2.06, -0.18)	0.02

To investigate the pairwise comparisons between each group, we performed a post-hoc Tukey HSD test (Figure 13).

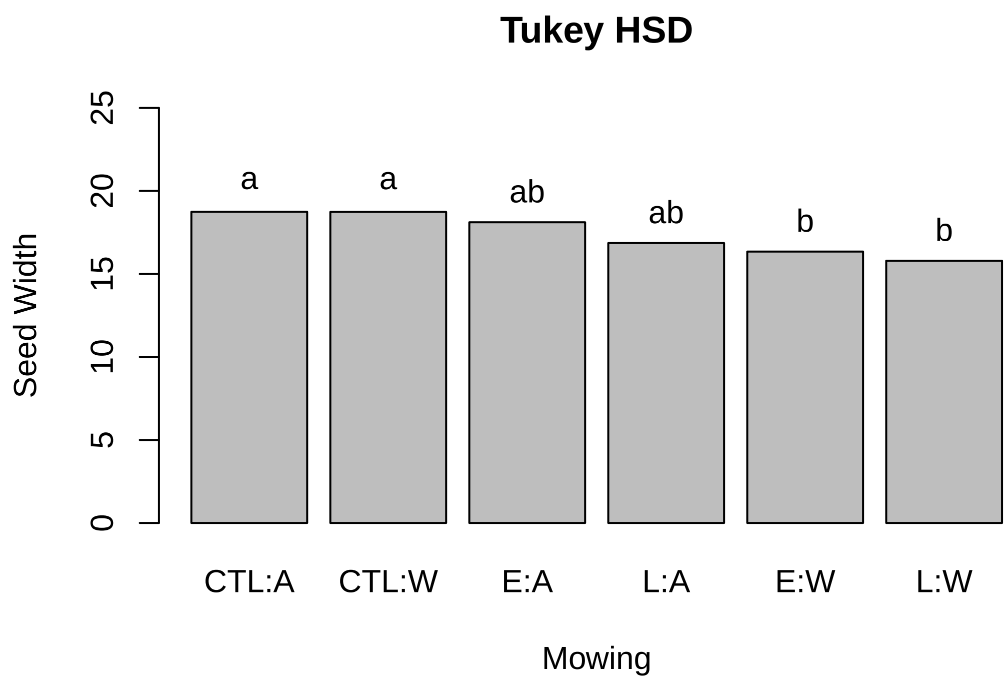


Figure 13: Results of post-hoc Tukey HSD test. Letters indicate groups which are significantly different, where 0.05 is the significance level. Notation is as follows: CTL - no mowing, E - early mowing, L - late mowing; A - ambient (i.e. no warming), W - warming

These results suggest that there are two major groups which emerge: (1) non-mowed, control plants regardless of whether they were warmed and (2) warmed plants that were mowed, regardless of the timing of the mowing. Because the timing of the mowing does not appear to be a significant factor in determining seed width, we fit a second model predicting seed width based on warming and a binary mowing variable.

Table 9: Results of partial F-test performed for models predicting seed width using warming and binary mowing predictors.

Model	P.Value
`Warming Only`	
`Warming and Mowing`	0.0161

Model	P.Value
`Interaction`	0.0828

Table 10: AIC and BIC for models predicting seed width using warming and binary mowing predictors.

Model	AIC	BIC
`Mowing Only`	2184.213	2189.426
`Warming Only`	2188.787	2194.000
`Warming and Mowing`	2180.400	2187.351
`Interaction`	2179.354	2188.042

Discerning between the `Warming and Mowing` and the `Interaction` models is less clear in this case. On one hand, the partial F-test suggests the `Interaction` model may provide a slightly better fit (Table 9) and the `Interaction` model has the lowest AIC value (Table 10), but the `Warming and Mowing` model has the lowest BIC value (Table 10). This result is consistent with our expectations, as a slight improvement in model fit may not be enough to overcome the BIC penalty for an additional term in the `Interaction` model.

The results of both models are summarized in Table 11. In the `Warming and Mowing` model, both treatments decrease seed width; whereas when an interaction term is added, neither the warming nor mowing terms are significant, but the interaction term itself becomes significant at a significance level of 0.1.

Table 11: Results of `Warming and Mowing` and `Interaction` models, respectively.

	`Warming and Mowing` Estimate	Pr(>|t|)	`Interaction` Estimate	Pr(>|t|)
Intercept	19.3284 (18.4, 20.26)	0	18.7442 (17.6, 19.88)	0
Mow	-1.6198 (-2.61, -0.63)	0.0013	-0.718 (-2.13, 0.7)	0.3194
Warm	-1.1485 (-2.09, -0.21)	0.0164	-0.0071 (-1.6, 1.59)	0.993
Mow:Warm			-1.7398 (-3.71, 0.23)	0.0828

These two results suggest that plants which are both warmed and mowed have smaller seed width. Plants which are both warmed and mowed are likely driving the significant mowing and warming coefficients we see in the `Warming and Mowing` model. Another post-hoc Tukey test, shown in Figure 14, supports this conclusion.

Discussion

The results of this experiment contribute to our understanding of how *Carduus nutans* may spread under future climates, and further how mowing management may mediate these changes. We found that, as predicted by physical models[4], the width of the seed is a good predictor of terminal velocity. Smaller seeds fall faster, and thus disperse shorter distances.

Theoretical[5] and experimental[6] results suggest that plants under stress will disperse farther, and our results are consistent with this idea. We showed that early mowing decreased terminal velocity, which means, with all else equal, these mowed plants will disperse further. Understanding the effect of late mowing on seed terminal velocity was difficult because many of the late mowed plants died. Fewer data points paired with small effect sizes for late mowed plant terminal velocity created wide confidence intervals and high p-values. Quantifying such terminal velocity changes in late-mowed plants may require a study with more replication to ensure sufficient statistical power after plant mortality due to late mowing.

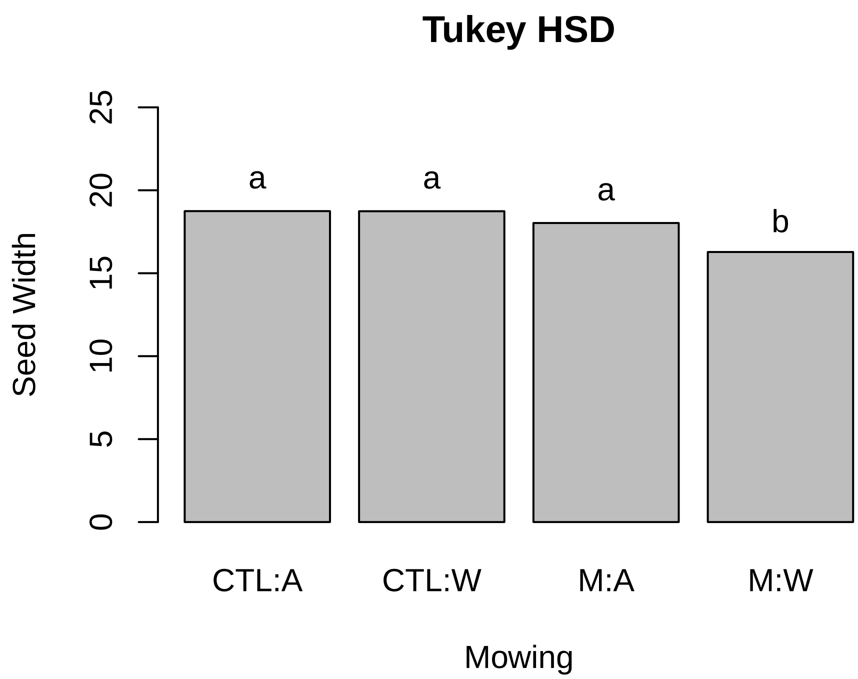


Figure 14: Results of post-hoc Tukey HSD test. Letters indicate groups which are significantly different, where 0.05 is the significance level. Notation is as follows: CTL - no mowing, M - mowing; A - ambient (i.e. no warming), W - warming

We also found that warming increased terminal velocity. In this case, all else being equal, we would expect seeds to disperse less far. However, previous work in our lab[7] showed that warmed thistles reach taller heights. Given a fixed terminal velocity, seeds of taller plants are expected to disperse further. Thus, an increase in terminal velocity of warmed plants does not necessarily translate directly into less dispersal and spread. Further modeling, that includes changes in plant height as well as changes in terminal velocity, will quantify overall changes in thistle spread.

We showed that plants which were both warmed and mowed had smaller seed width. Based on our model which describes terminal velocity as a function of seed width (Research Question 1), we expect these warmed and mowed plants to have higher terminal velocity and, therefore, to disperse less far. Yet, in our analysis of changes in terminal velocity by treatment (Research Question 2), we showed mowing decreased terminal velocity. These discrepencies suggest that treatment level changes in seed terminal velcotiy cannot be fully explained by changes in seed width.

This data set is lacking seed mass data, which may be responsible for the inconsistencies we observed. Seed mass is a second physical property needed to predict terminal velocity[4] and may also change with warming and mowing. Lacking seed mass data limits our ability to explain changes in seed terminal velocity through physical properties of the seed. However, our results which quantify the effect of the treatments on terminal velocity are unaffected, Further studies which measure both seed width and seed mass will be necessary to explain physical and biological mechanisms which explain the observed changes in terminal velocity.

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