

Monitoring the Phenology of *Chromolaena odorata* to Inform Management of an Incipient
and Highly Invasive Species in Hawai‘i

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Table of Contents

Abstract.....	3
Motivation.....	4
Background.....	4
Objectives	6
Methods.....	7
<i>Greenhouse germination trials</i>	8
<i>USA Standardized Phenology Monitoring Methods</i>	8
<i>Reproductive Phenophase Output and Plant Condition</i>	9
<i>Data Analysis</i>	9
Results.....	10
<i>Phenological activity of C. odorata in KTA</i>	10
<i>Relationship between phenophases of C. odorata and precipitation</i>	11
<i>Relationship between phenophases of C. odorata and temperature</i>	12
<i>Relationship between reproductive phenophase output and average plant condition</i>	13
<i>Relationship between reproductive phenophase output and seed germination</i>	13
Discussion.....	16
Conclusion	18
References.....	20

Abstract

The invasion of nonnative species has negative impacts on ecological processes and ecosystem services, and these impacts are being exacerbated by global trade and climate change. In Hawai‘i, invasive species, along with associated biodiversity loss and habitat degradation, are the greatest threat to the archipelago’s endemic biota. In 2011, *Chromolaena odorata* (Devil’s Weed), a globally dispersed invasive species, was first detected in the Kahuku Training Area (KTA) on the Island of O’ahu. Known as one of the world’s worst weeds, *C. odorata* is an aggressive colonizer of disturbed environments that, once established, creates dense monotypic stands that prevent the growth and regeneration of other species. Since its discovery in 2011, *C. odorata* has spread to occupy ~1,042 ha in KTA. The objective of this study was to develop a *C. odorata* phenology monitoring program to investigate the correlation between observed phenophases, seed germination, and climate variables to inform integrated weed management (IWM). To address this objective, I monitored the phenology (i.e., phenophases or life cycle events) and plant condition of *C. odorata* every two weeks in KTA for 12 months in five study sites and recorded monthly precipitation and temperature from the closest weather station. In addition, I collected soil samples in each study plot monthly and monitored seedling emergence in the greenhouse over 12 months. Overall, I found that flowering occurred between November – February and fruit set occurred between February – April, with smaller flowering and fruiting events in May – June and June – July, respectively. Monthly precipitation and temperature had strong explanatory power for both overall plant condition and productivity-related phenophases (i.e., flower production and seed drop). In addition, a positive correlation existed between seedling germination and the presence of flowers. Based on this information, chemical and mechanical control should be conducted between August and October to reduce large flowering events beginning in November. Overall, the results of this study will allow for the adjustment and optimization of IWM practices for this species based on phenophases that are more susceptible to weed control methods, as well as informing the use of phenology in controlling and managing invasive species more broadly.

Keywords: climate; integrated weed management (IWM); land management; plant control; restoration

Motivation

The introduction of invasive species has negative impacts on ecological processes, ecosystem services, and local and national economies, and these impacts continue to increase with global trade and climate change (Poland et al., 2021). Their establishment alters the structure and function of native ecosystems and, ultimately, can lead to species extinctions (Poland et al., 2021). Invasive species, along with associated biodiversity loss and habitat degradation, are the greatest threat to Hawai‘i’s endemic flora and fauna (Daehler et al., 2004). Hawai‘i provides habitat to over 44% of all species on the U.S. endangered and threatened plant species list, with 25% of these species found only in Hawai‘i. According to Poland et al. (2021), the term invasive species indicates a nonnative species whose presence does or is likely to cause economic or environmental harm, or harm to human health. Understanding how invasive species interact with their environment can help anticipate their impacts, as well as inform protection of native species and habitats at risk (Morais & Freitas, 2015).

In 2011, *Chromolaena odorata*, known as Siam Weed or Devil’s Weed, was first detected in the Kahuku Training Area (KTA) on the Island of O‘ahu. Known as one of the world’s worst weeds, *C. odorata* is an aggressive colonizer of disturbed environments such as roadsides, abandoned agricultural fields, and degraded forests (Zachariades et al., 2009). Once established, it creates dense monotypic stands that prevent the growth and regeneration of other species, due at least in part to allelopathic qualities (Zachariades et al., 2009). Though not as widely distributed in Hawai‘i as other, more established invaders, due to *C. odorata*’s invasiveness in other areas globally, it has a very high potential to increase widely outside of its current habitat, making early control critical.

Since its discovery in 2011, *C. odorata* continues to be the top incipient priority for the Army Natural Resources Program-O‘ahu (ANRPO). Currently, ANRPO manages 54 *C. odorata* incipient control areas (ICAs; weed control efforts with the goal of eradication of a particular invasive species) spanning both the Wai‘anae and Ko‘olau Mountain Ranges. Each ICA is species-specific and geographically defined. Of the 54 ICAs, 26 are located in KTA, where it has spread to occupy ~1042 ha (Figure 1) and accounted for 54% of time spent on incipient control efforts conducted by ANRPO in the 2021 reporting year (total of 2355 people hours). Despite the resources and time put towards controlling *C. odorata*, due to its large infestation across difficult terrain *C. odorata* continues to spread. To better manage this incipient invasive species, more applied management options are needed to optimize current and future control efforts.

Background

Chromolaena odorata is a fast-growing herbaceous to woody perennial plant in the family Asteraceae (Gautier, 1992). Native to South and Central America, *C. odorata* forms dense tangled bushes up to 2 m high, with the ability to branch and grow on surrounding vegetation to up to 20 m high. Leaves are opposite, ovate-triangular, with serrated margins, and a distinctive 3-vein “pitchfork” pattern. Due to its ability to asexually form viable seeds, also known as apomixis, plants can germinate and set seed within a 12-month period and are able to produce up

to 800,000 seeds per individual plant per year (Witkowski & Wilson, 2001). The small seeds are then dispersed long distances by wind, as well as by adhesion to fur, feathers, vehicles, and clothes. Steroids and other toxins produced by the plant make it toxic to livestock and reduce the growth of other surrounding plants via allelopathy (Zachariades et al., 2009).

C. odorata is a serious invasive species in other parts of the world, where it threatens food security and the integrity of ecological systems in West Africa, Asia, and the Pacific. For example, *C. odorata* was introduced into West Africa in the late 1930s in Ghana, and since then has spread to occupy 12 of the 16 countries in Africa, where it is considered one of the worst invasive species as a result of significant impacts to native ecosystems and agriculture (Aigbedion-Atalor et al., 2019). The invasiveness of *C. odorata* is due to its high reproductive capacity and dispersal of propagules, adaptation to growth in a range of soil types and climate conditions (Aigbedion-Atalor et al., 2019), ability to outcompete and prevent the natural regeneration of native plants (Honu & Dang, 2000; Timbilla & Braimah, 2000), and its ability to rapidly invade new areas where it significantly reduces the biodiversity of native ecosystems (Timbilla & Braimah, 2000). As chemical and mechanical control methods are often deemed unsustainable, costly, and ineffective, biological control agents have been released to control *C. odorata* outside of Hawai‘i. A gall fly species *Cecidochares connexa* (Tephritidae), has been shown to significantly reduce the density of *C. odorata* in Papua New Guinea, Indonesia, and parts of West Africa. *C. connexa* is indigenous from the USA to central South America, and is known to be highly host specific to *C. odorata* (Aigbedion-Atalor et al., 2018). *C. connexa* is currently being tested in Hawai‘i, with the goal of establishing the first gall fly colony in the coming years to help reduce the density of *C. odorata* in the state.

Though biological control is often seen as the most environmentally friendly and cost-effective way to manage a widely spread invasive species, the combination of one or more control methods that consider the biology or phenology of the target species can lead to more successful control via synergistic effects (Lake & Minter, 2018). Integrated weed management (IWM) is a sustainable approach to managing invasive species that combines biological, chemical, and mechanical methods in a way that maximizes effectiveness while minimizing costs and environmental impacts (Paynter & Flanagan, 2004). As an adaptive management approach, IWM requires sufficient knowledge of the ecology and phenology of the species and the invaded system to better predict the outcome of control efforts. *C. odorata* has been documented to flower in December to January in the northern hemisphere, and flowering is typically triggered by decreases in rainfall and day length (Zachariades et al., 2009). However, flowering has been observed anecdotally in KTA from January to March, highlighting that region-specific information is needed on *C. odorata* phenology in Hawai‘i to inform IWM.

Phenology is the study of seasonal activities of organisms (e.g., flowering, leaf flush, etc.) that is central to understanding ecological interactions between species and the ecosystems they inhabit (Denny et al., 2014). Phenology monitoring has many useful applications, including delineating the response of vegetative and reproductive stages to climate and optimizing the timing of management practices. Plant phenology can also help to provide insight on

management strategies for opportunistic and competitive invasive species (Hernandez, 2019). For example, a study conducted by Taylor et al. (2020) documented the timing of phenophases of *Verbesina encelioides* (golden crownbeard) on Midway Atoll NWR to improve eradication efforts. Using a general phenology monitoring approach developed by the USA National Phenology Network (USA-NPN), which defines the term phenophase as “an observable stage or phase in the annual life cycle of a plant or animal that can be defined by a start and an end point (Denny et al., 2014)”, this phenological monitoring revealed that *V. encelioides* can set seed in as little as 31 days, which was then used to adjust treatment schedules in infested areas to every 30 days. The adjustment of treatment schedules based on phenology data is now an important tool in maintaining low frequency and density of *V. encelioides* across Midway Atoll NWR (Taylor et al., 2020).

Studying the phenology of invasive species can also aid in better understanding the physiological and morphological adaptive strategies that species utilize to capture resources (Morais & Freitas, 2015). A study by Wallace et al. (2016) tracked the phenology of *Pennisetum ciliare* (buffelgrass), an aggressive invasive species in the Sonoran Desert in southern Arizona, USA, to identify periods of reproduction and green-up, where plants are most susceptible to mechanical removal and herbicide application. Herbicide treatments were then optimized to be applied 1-2 weeks following a precipitation threshold when plants are 50% more green. Phenology monitoring can, therefore, help to identify how species will respond to environmental changes, which natural resource managers may then use as indicators to implement control strategies that focus on targeting life cycles most susceptible to control. Therefore, my project focused on understanding the correlation between observed phenophases of *C. odorata* and climate variables to better predict phenology of the species based on readily available climate data.

Objectives

This study sought to investigate how a phenology monitoring program for *C. odorata* can help to better inform the use of IWM to successfully manage this problematic invasive species in Hawai‘i. Specifically, this project addressed three questions: (1) What is the relationship between phenophases of *C. odorata* and climate variables (e.g., current precipitation and temperature)?; (2) What correlations exist between reproductive phenophase outputs of *C. odorata* and its seed germination in the greenhouse?; and (3) What is the relationship between reproductive phenophase output and plant condition?

Methods

I monitored *C. odorata* phenology in KTA for one year from February 2021 to January 2022. KTA is a 9,400 acre military base located on the northern tip of the moku of Ko‘olauloa on the island of O‘ahu, Hawai‘i. KTA has an elevation range between 6 to 640 m, where it stretches from the Ko‘olau summit to lower elevations dominated by alien vegetation that experience regular disturbances by military training and recreational use (e.g., motocross). KTA spans multiple ahupua‘a (i.e., Kaunala, Waiale‘e, Pahipahiālua, ‘Ōpana, Kawela, Hanaka‘oe, ‘Oi‘ō, Ulupehupehu, Punalau, Kahuku, Keana, Māleakahana) with the core infestation of *C. odorata* between Kaunala and Pahipahuālua gulches. Higher elevation soils are mainly composed of Oxisols, while the lower elevations include Ultisols and Mollisols (Hawai‘i Soil Atlas).

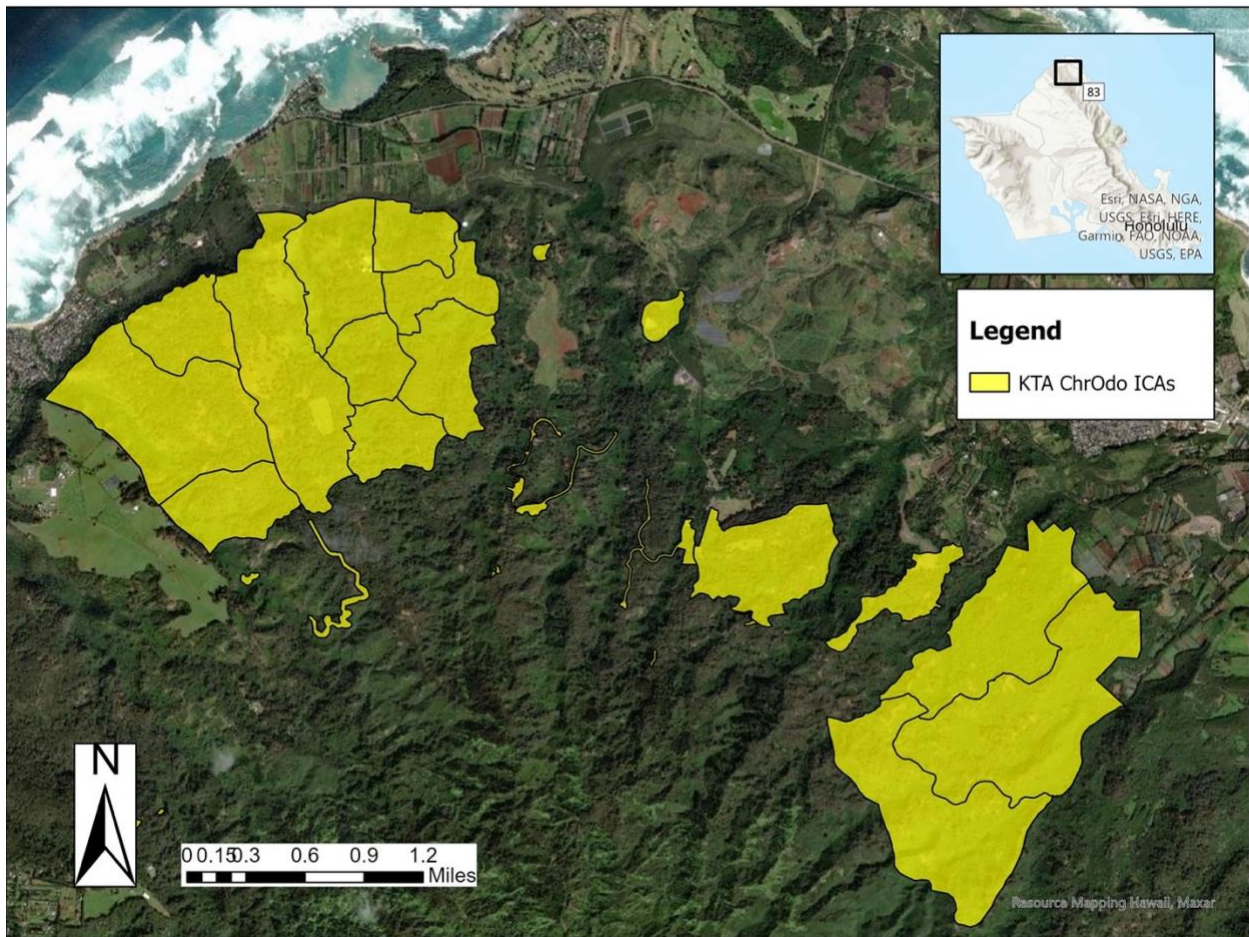


Figure 1. Map of *C. odorata* incipient control areas (ICAs) in Kahuku Training Area. Borders depict individual ICAs.

I selected five 10 x 10 m study plots that were easily accessible and 5 meters away from roads or motocross trails, with a total of 15 individual plants in each plot ($n=75$), located in areas of KTA that consist of highly disturbed nonnative vegetation, such as koa haole (*Leucaena leucocephala*), guinea grass (*Megathyrsus maximus*), ironwood (*Casaurina equisetifolia*), and strawberry guava (*Psidium cattleianum*). Using standardized phenology monitoring methods

developed by the USA-NPN, I documented the onset, duration, and intensity of observed *C. odorata* phenophases (see below) on individual plants in each plot every two weeks for one year.

Greenhouse germination trials

I collected soil samples in each of the five study plots monthly to follow seedling emergence in the greenhouse. Three soil samples were taken from each study plot at a depth of 10 cm using a soil probe and composited within a plot. Composite soil samples from each individual plot were transported to the ANRPO greenhouse and placed in individual soil trays for germination trials. Individual soil trays received daily watering and consistent light under a shade cloth. Emerging *C. odorata* seedlings were identified, recorded, and immediately removed from the soil trays for the duration of the study.

USA Standardized Phenology Monitoring Methods

The protocols developed by the USA-NPN are standardized within taxonomic plant groups and utilize phenophases that are easily observable, responsive to seasonal changes, and accurately reflect species life histories (Denny et al., 2014). The observation protocol applies a status monitoring approach, in which observers visit a site at a regular interval to monitor and record the phenological status of marked individuals (Rosemartin et al., 2018).

For my project, I tagged 15 individual plants in each plot, numbered 1 thru 15. During each site visit, I observed the presence, absence, and intensity of each phenophase (i.e., initial growth, leaves, flower or flower buds, open flowers, fruits, ripe fruits, and recent fruit or seed drop). Recording the presence or absence of each phenophase allows for capturing the absence of data when the phenophase is not occurring and during repeat events, in contrast to traditional monitoring of annual “first” events (Rosemartin et al., 2018). According to Rosemartin et al. (2018), the intensity can be described as a “categorical measure indicating the extent to which a phenophase is expressed for an individual plant observed on a given visit (e.g., percentage of flowers open)”. Rather than simply recording the presence of open flowers on an individual plant, observing the intensity allows, for example, documentation of the total number of flowers and the proportion of flowers that are open (Denny et al., 2014).

Relationship between Phenophases and Climate Variables

Alongside the documentation of observed phenophases, I recorded the average, low, and high monthly temperature, and total monthly precipitation from the closest weather station to my study plots (Sunset Beach Earth Station); www.wunderground.com). Observing the phenophases of *C. odorata* via an established phenology monitoring program allows for determining the relationship between climate variables and the timing of phenological transitions of *C. odorata*. Once this relationship is established, these models can then be used to produce real-time and short-term forecast maps of the timing of phenological transitions to directly support science-driven management decisions (Crimmins et al., 2017). Predicting when *C. odorata* will undergo a phenological transition in KTA is valuable for the implementation of IWM strategies. For

example, optimal timing of management activities such as chemical treatment will benefit from real-time information and short-term forecasts of phenological transitions. To determine how climate in the year that I collected data compared to average climate for my study site, I compared the average, low, and high temperature and total precipitation from 1990-2018 from the Sunset Beach Earth Station to climate conditions in my study year. Statistical analysis using the Cumulative Distribution Function (CDF) in R ver. 4.0.4 (R Core Team, 2021) determined that my study year climate variables were characteristic of the 28-year averages.

Reproductive Phenophase Output and Plant Condition

I identified reproductive phenophase output as the average occurrence of each reproductive phenophase (i.e., Flowers/Flower Buds, Open Flowers, Fruits, Ripe Fruits, Seed Drop). This was calculated by dividing each occurrence over the total number of site visits to obtain an average percentage. Alongside the documentation of phenophases, I also recorded the plant condition for each individual plant during each scheduled monitoring visit. Plant condition was determined as Poor (1), Moderate (2), and Healthy (3).

Data Analysis

I used a Generalized Linear Model (GLM) to assess the relationship between phenophases and current temperature and precipitation. To assess the relationship between seed germination and reproductive phenophase output, I calculated the average number of seedlings that emerged per study plot and utilized Linear Regression. I also used Linear Regression to assess the relationship between reproductive phenophase output and average plant condition. All statistical analysis was performed using R ver. 4.0.4 (R Core Team, 2021) with a significance level of $\alpha = 0.05$.

Results

Phenological activity of C. odorata in KTA

The presence of leaves and initial growth occurred year-round in KTA for *C. odorata* (Figure 2). Flowering had a bimodal distribution, occurring between November – February, and to a somewhat smaller scale in May - June. Fruiting also exhibited a bimodal distribution and occurred in February – April, and a smaller event in June – July. Seed drop occurred between February – July. There was no reproductive activity observed between August – October. Although flowering and fruiting both exhibited a bimodal distribution, Figure 3 demonstrates that the first events of both phenophases had the greatest intensity, followed by a much smaller intensity scale in the second event. This may be due to only a handful of plants exhibiting either a late flowering event or another occurrence of flowering, followed by fruiting.

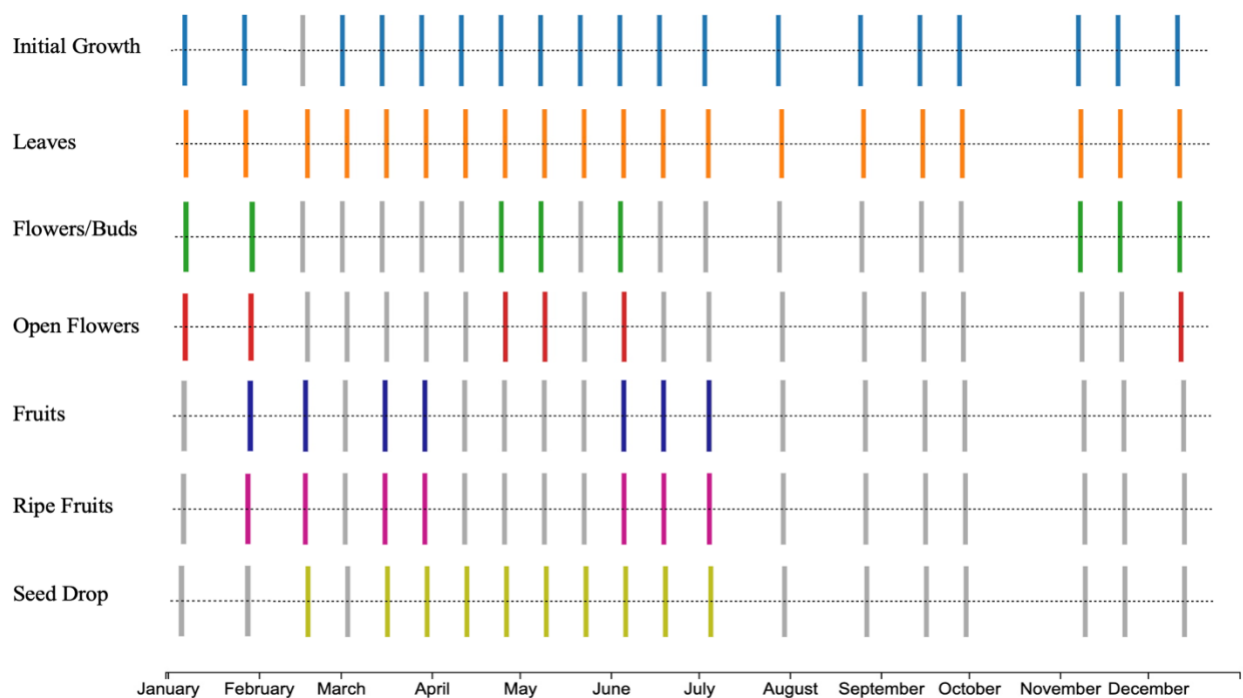


Figure 2. Phenological activity (presence/absence) for *C. odorata* in Kahuku Training Area, observed from February 2021 to January 2022. Colored bars represent the presence of observed phenophases, whereas gray bars represent the absence of phenophases.

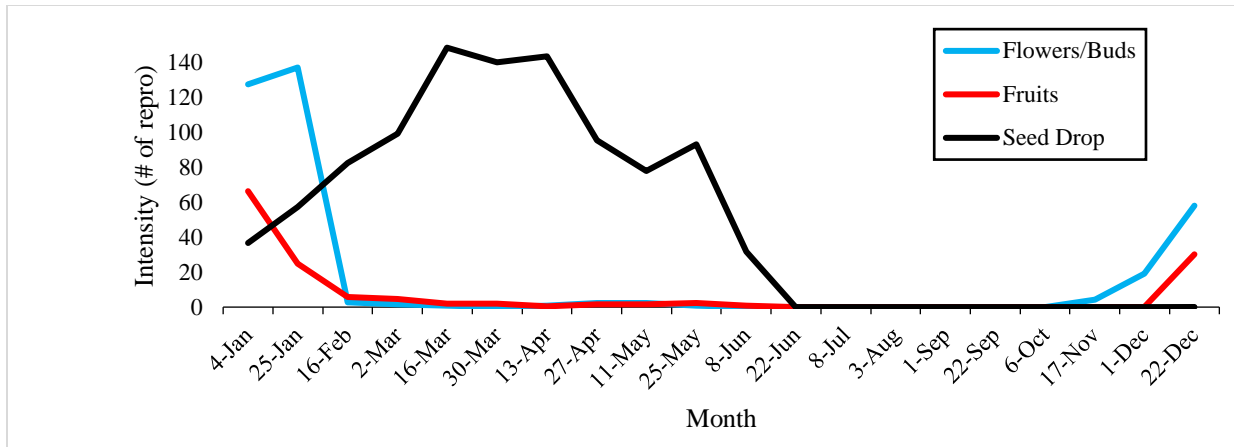


Figure 3. Average intensity of reproductive phenophases for *C. odorata* in Kahuku Training Area, observed from February 2021 to January 2022.

Relationship between phenophases of C. odorata and precipitation

There was a significant positive relationship between precipitation and Flowers/Buds (Figure 4), Open Flowers, Fruits, and Ripe Fruits phenophases (Table 1). There were a few occurrences of heavy rainfall during the year (Figure 5), that may be correlated with the onset and duration of both flowering and fruiting of *C. odorata*, which occurred from November – July. These rainfall events mainly occurred during the wet season, while the summer months between July – September experienced little to no rainfall and reproductive phenophase activity. These results illustrate that an increase in precipitation may trigger the onset and duration of both flowering and fruiting of *C. odorata* in KTA.

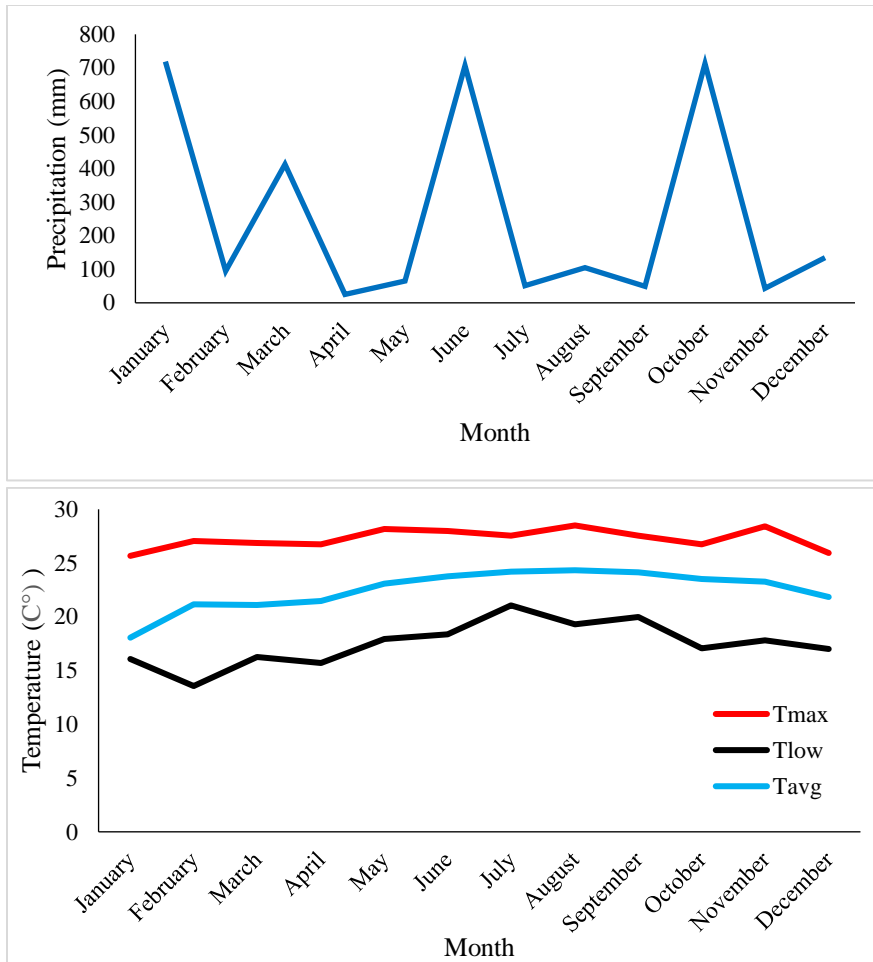


Figure 4. Total monthly precipitation (mm) and monthly high, low, and average temperatures (C°) recorded from the Sunset Beach Earth Station (February 2021 to January 2022).

Relationship between phenophases of C. odorata and temperature

There was a significant negative relationship between temperature and reproductive phenophases (i.e., Flowers/Buds, Open Flowers, Fruits, Ripe Fruits, Seed Drop). Based on temperature readings from the Sunset Beach Earth Station, the highest average monthly temperatures ranged between 24.1-24.3°C from July-September. There appears to be a vegetative (growth) stage of *C. odorata* in Hawai‘i that occurs between July-October, where the occurrence of reproductive phenophases are absent (Figures 2 and 3). These results reveal that *C. odorata* has a seasonality, where its vegetative (growth) stage occurs during the dry season, followed by the rainy season where increasing precipitation triggers the onset of flowering.

Table 1. Linear regression analysis results for relationships between phenophases and climate variables ($\alpha = 0.05$).

	Phenophase	β	Std Error	Z value	p value
Precip	Flowers/Buds	0.002	0.0002	7.168	<0.001
	Open Flowers	0.004	0.0004	11.48	<0.001
	Fruits	0.0005	0.0002	2.28	<0.05
	Ripe Fruits	0.0005	0.0002	2.07	<0.05
T_{avg}	Flowers/Buds	-0.763	0.0465	-16.39	<0.001
	Open Flowers	-1.063	0.0647	16.44	<0.001
	Fruits	-0.419	0.0364	-11.52	<0.001
	Ripe Fruits	-0.404	0.0367	-11.02	<0.001
T_{low}	Flowers/Buds	-0.449	0.0451	-9.98	<0.001
	Open Flowers	-0.445	0.0565	-7.87	<0.001
	Fruits	-0.972	0.0699	-13.91	<0.001
	Ripe Fruits	-0.903	0.0664	-13.59	<0.001
	Seed Drop	-0.317	0.0342	-9.252	<0.001
T_{high}	Flowers/Buds	-2.009	0.1211	-16.6	<0.001
	Open Flowers	-3.211	0.2561	-12.54	<0.001
	Fruits	-0.496	0.0782	-6.35	<0.001
	Ripe Fruits	-0.484	0.0798	-6.066	<0.001
	Seed Drop	0.432	0.0638	6.78	<0.001

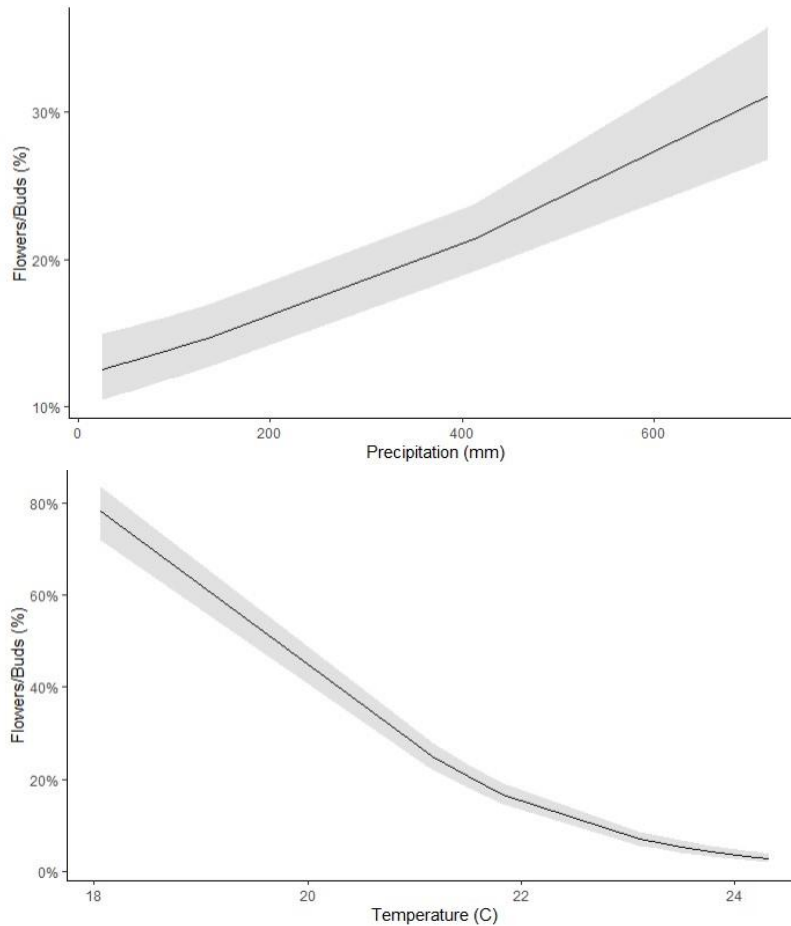


Figure 5. Predicted values (marginal effects) from the Generalized Linear Model illustrating the relationship between Flowers/Buds phenophase and Temperature (C°), and Flowers/Buds phenophase and Precipitation (mm).

Relationship between reproductive phenophase output and average plant condition

Results showed that there was a significant positive relationship between the reproductive phenophase output and average plant condition (Table 2). Healthier plants exhibited reproductive phenophases longer than less healthy plants during the year (Figure 6). These results may be due to habitat characteristics in study plots that are more suitable to *C. odorata*, which in turn allowed plants to reproduce at a higher intensity and longer period.

Relationship between reproductive phenophase output and seed germination

There was a significant positive relationship between the average seedling germination and Flowers/Flower Buds ($\beta=0.137$, $F=5.792$, $p<0.05$) and Open Flowers ($\beta=0.139$, $F=11.78$, $p<0.001$) phenophases (Table 2). Although there was a significant positive relationship, results may be inconclusive due to a small number of seedlings that emerged in the greenhouse. The slope of the relationship for Flowers/Buds and Open Flowers was $\beta=0.14$, which is very low and indicates that an increase in reproductive phenophase output only had a marginal impact on seedling germination.

Table 2. Linear regression analysis results for the relationship between average plant condition and reproductive phenophase output, and the relationship between seedling germination and reproductive phenophase output ($\alpha = 0.05$).

	Reproductive Phenophase	β	F statistic	p value
Average Plant Condition	Flowers/Buds	0.273	20.32	<0.001
	Open Flowers	0.188	16.83	<0.001
	Fruits	0.199	6.43	<0.05
	Ripe Fruits	0.2102	7.08	<0.01
	Seed Drop	0.224	4.02	<0.05
Seedling Germination	Flowers/Buds	0.137	5.79	<0.05
	Open Flowers	0.139	5.79	<0.001

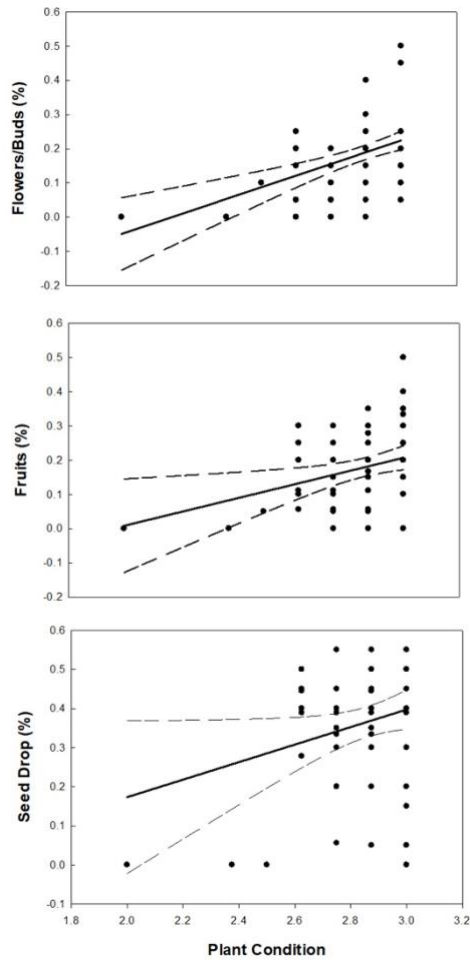


Figure 6. Relationship between reproductive phenophase output (%) and average plant condition. Increasing plant condition indicates healthier plants.

Discussion

This study sought to investigate how a phenology monitoring program for *C. odorata* can help to better inform the use of IWM to successfully manage this highly invasive species in Hawai‘i. I focused on understanding the relationship between observed phenophases of *C. odorata* and climate variables to better predict the phenology of the species based on readily available climate data. After monitoring the phenology of *C. odorata* in KTA for one year, I found that flowering and fruiting had a bimodal distribution. Flowering occurred from November – February, and May – June, while fruiting occurred from December – April, and May – July. Seed drop occurred from February – July, followed by no reproductive activity occurring from August – October. Although there was a bimodal distribution of flowering and fruiting, Figure 3 highlights that the first event of both phenophases had the greatest intensity, followed by a much smaller event. This may be due to only a handful of plants flowering and fruiting twice in the same season or occurring at a later event. Future monitoring should look further into this bimodal distribution to determine if results are consistent or if there is only one main flowering and fruiting event.

Relationship between observed phenophases of C. odorata and climate variables

I found that there was a significant positive relationship between precipitation and the phenophases of Flower/Buds, Open Flowers, Fruits, and Ripe Fruits. Results demonstrate that precipitation events are associated with the onset and duration of flowering. During the study period, October experienced a high amount of total monthly precipitation (Figure 5). This large rainfall event was then followed by the onset of flowering that occurred in November. Another rainfall event occurred in January (Figure 5), where the intensity of both Flowers/Buds and Fruits were highest (Figure 3). According to Gautier (1993), *C. odorata* flowers in the dry season, triggered by decreases in both day length and rainfall. Although there was a large rainfall event that occurred in June, which was then followed by no reproductive activity, my results suggest that flowering of *C. odorata* in Hawai‘i may be triggered by the onset of precipitation caused by the rainy season. Future monitoring of *C. odorata* should continue to analyze this relationship further to determine what the precipitation threshold is to initiate reproductive phenophases, and if the species here truly behaves differently than in other parts of the world where it is more intensely studied.

I also found that there was a significant negative relationship between average monthly temperature and the phenophases of Flowers/Buds, Open Flowers, Fruits, and Ripe Fruits. These results may be associated with the vegetative stage that *C. odorata* exhibited from August – October, where no reproductive phenophases occurred. During the study year, July – September experienced the highest average monthly temperatures, demonstrating how the increase in temperature may be associated with the decrease in occurrence of reproductive phenophases.

Although climate in this study year was in line with the past 28-year average, it would be useful to continue monitoring the phenology of *C. odorata* in Hawai‘i to identify how the species may react to changing climate and individual events, such as early seasonal precipitation or high temperatures. Shi et al. (2021) found that warming facilitated the success of *C. odorata* placed in

a series of artificial multispecies communities. Consistent with prior studies that have identified how invasive species have a higher stress tolerance, plasticity, and resource utilization efficiency than native species, this prior study demonstrated that warming enhanced *C. odorata* invasiveness and decreased the productivity of the native community (Shi et al., 2021). Although my project did not look at the relationship between climate change and invasiveness, future studies will be able to incorporate my baseline study of the phenology of *C. odorata* in Hawai‘i to better predict how the species will behave under changing climates.

By understanding how climate variables such as precipitation and temperature interact with plant phenology, natural resource managers can better predict how species will behave and be able to adjust treatment schedules to optimize control efforts. Based on my results, I suggest that ANRPO and other conservation organizations that manage *C. odorata* should adjust their treatment schedules to be conducted from August – October, where reproductive phenophases are not occurring and before flowering begins. Currently, control schedules are based on the goal of treating each ICA at least twice a year, and by other external factors such as staff time and access into KTA. By controlling *C. odorata* from August – October, it would not only reduce treatment from twice a year to only once a year, but also prevent the spread of seeds and reduce the overall density by controlling plants before they flower and reproduce.

Relationship between reproductive phenophase output and seedling germination

I found that there was a significant positive relationship between reproductive phenophase outputs and seedling germination. Although my results were significant, they were also associated with a low slope, demonstrating that reproductive phenophase output only had a marginal impact on seedling germination. This may be due to the low number of seedlings that germinated in the greenhouse during the study period. Future studies should record seedling emergence in each study plot during phenophase monitoring visits to allow resource managers to identify which phenophase is associated with significant seedling emergence. This will allow for a better understanding of germination predictions to improve the timing of seedling management. For example, if seedling emergence was high during a specific phenophase, it would allow resource managers to adjust their treatment schedules based on the known phenology of *C. odorata* in Hawai‘i.

Future monitoring of C. odorata in Hawai‘i

Phenology data can facilitate the success of natural resource management goals and support informed decision making (Enquist et al., 2014). It allows managers to improve their understanding of species interactions and optimized windows for chemical and mechanical control. For example, Jucker et al. (2020) wanted to understand the seasonal variation in the growth phenology of stinking passionflower (*Passiflora foetida*) in Northern Australia and identify the optimal time window for management. The authors found that there was a rapid increase in mean leaf size following two rainfall events. This information was then used to create an adaptive management plan by applying the most effective combination of treatment methods

two months after a large rainfall event, when stinking passionflower was at its peak in terms of vegetative growth.

Although my project studied the phenology of *C. odorata* in Hawai‘i for one year, there remains a need for coordinated, long-term monitoring and research of key environmental variables as this species is currently found in areas in the state that differ in climate, soils and vegetation. For example, monitoring phenology is a key indicator of climate change impacts (Enquist et al., 2014). Long-term monitoring will improve understanding of how *C. odorata* will respond to seasonal variations and further inform adaptive management plans. Future studies may continue monitoring phenology and identify which phenophases are most susceptible to chemical and mechanical control. This will allow for the adjustment of treatment schedules that will allow for the optimization of both staff time and resources in controlling *C. odorata*.

The information presented here will also be useful for informing the future release of the biocontrol *C. connexa* in Hawai‘i. Aigbedion-Atalor et al. (2018), who studied the success of *C. connexa* in Ghana, observed a low density of *C. connexa* in the dry season. This was not unexpected because of the susceptibility of the gall fly to dry climatic conditions that had previously been reported. However, the persistence and recovery of *C. connexa* over the period of the study indicated that the agent is capable of surviving through the dry season in Ghana (Aigbedion-Atalor et al., 2018). Based on suggested adjustments of treatment schedules to optimize efforts to control *C. odorata*, future IWM strategies should take into account both the phenology of *C. odorata* and observed behavior of the biocontrol. For example, herbicide treatments should be conducted between August – October, where reproductive phenophases are not occurring and possibly when *C. connexa* will be in low densities.

Only one-third of biocontrol programs for invasive species are successful (Buckley et al. (2004). Other management options are, therefore, needed, such as IWM, which emphasizes the use of several complimentary control measures. In a study conducted by Buckley et al. (2004), the authors used models of increasing complexity to determine the most successful parameters for controlling an invasive shrub (*Mimosa pigra*), in tropical Australia. The models demonstrated that biocontrol alone is only successful at low levels of small scale disturbance and seedling survival, and would take decades to reduce a stand to <5% site occupancy (Buckley et al., 2004). The most successful IWM strategy was an application of herbicide in year one, mechanical and fire control in year two, herbicide in year three, and biocontrol along the edges of the invasion (Buckley et al., 2004). By integrating biological control with other treatments, such as chemical and mechanical control, management can not only significantly reduce the cost of managing *C. odorata*, but reduce the spread and density of the species in KTA and across Hawai‘i.

Conclusion

Studying the phenology of invasive species is a key strategy to better understanding seasonal life history events such as germination, growth, and reproduction that can strongly determine a species ability to utilize resources and reproduce (Godoy & Levine, 2014). By improving knowledge and literacy of phenological data and research, it will help land managers

achieve their goals of invasive species control by identifying points in the life cycle of species at which they are most susceptible to control, while protecting habitats that are at risk (Morais & Freitas, 2015). My project, which implemented a phenology-based monitoring program of *C. odorata* to better understand the relationships between phenophases and climate variables, will improve the use and integration of both invasive species management and IWM in Hawai'i. During my project, I was able to successfully add *C. odorata* onto the USA-NPN's Nature's Notebook species list. This will allow other scientists or volunteer observers to input their phenophase observations of *C. odorata* into USA-NPN's database, which will provide valuable long-term data for understanding phenological responses around the world. Not only will phenological data of *C. odorata* be more readily available to others but serve as an example on how studying the phenology of invasive species can directly support natural resource decision making.

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