THE UNIVERSITY OF QUEENSLAND

AUSTRALIA

Determining density thresholds for managing rabbit damage to broccoli and corn

Ruishu Wang

Bachelor of Life Science

A thesis submitted for the degree of Master of Philosophy at

The University of Queensland in 2019

The School of Agriculture and Food Sciences

Abstract

The European rabbit (*Oryctolagus cuniculus*) is one of the most successful invasive mammals in Australia, causing substantial economic losses in agriculture and damage to the environment. The Lockyer Valley in South East Queensland is an important vegetable growing region in Australia. Unlike most other regions of Australia where rabbits have been an endemic problem for a long time, rabbits invaded this region in 2009, causing increasing crop losses. Many rabbit control methods are available to vegetable growers, but there is no rabbit-density threshold available for managing damage to vegetable crops because little is known of how different densities of rabbits reduce crop yields. In this thesis, I aim to determine the density thresholds for managing rabbit damage to broccoli and corn crops, and to understand how the broccoli plant compensates for damage. This information will assist vegetable growers in developing an effective management strategy for rabbit control.

Known densities of rabbits (0, 3.75, 7.5, 15 and 30 rabbits per hectare) of rabbits were introduced into broccoli crops for a predetermined period of time (24 days) at different plant development stages (single-point damage), and yield losses caused by rabbits were measured. The study was conducted in rabbit and predator-proof enclosure at The University of Queensland (UQ) Gatton campus in 2014 and 2015. When rabbits were introduced to broccoli at the seedling stage (14 days after transplanting [DAT]), the relationship between introduced rabbit density (D_I) and yield loss (YL) was linear, with YL increasing with D_I. When rabbits were introduced at the establishment stage (28 DAT), there was no significant relationship between D_I and YL. Thus, rabbit control is most critical at the seedling stage. The density threshold (D_T) was estimated based on the relationship between D_I and YL at the seedling stage. D_T varied depending on the effectiveness of the control method in reducing D_I and on the cost of control as a percentage of the farm-gate value of broccoli. For example, D_T would need to be 6.54 rabbits per hectare for triggering RABBAIT® 1080 carrot baiting, if this method was effective in reducing D_I by 94% and if the cost of baiting was 1.01% of the farm-gate value of broccoli.

To assess the ability of broccoli crops to compensate for damage caused by rabbits, simulated rabbit damage was performed under greenhouse conditions at UQ Gatton campus from June 2015 to January 2016. Part of each leaf (equivalent to 5%, 10%, 25%, 50% and 80%) from each plant was removed manually to simulate these levels of canopy damage at the seedling stage (5 leaves, 17 DAT), establishment stage (7 leaves, 28 DAT)

and heading stage (11 leaves, 47 DAT). When damage was imposed at the establishment and heading stages, the broccoli plants could completely compensate for the damage and maintain yield. Broccoli that was damaged at the earlier stages of development did not completely recover from damage before harvest.

To assess the effects of rabbits grazing on corn, an experiment was conducted at rabbit- and predator-proof enclosures on the UQ Gatton campus over the summer cropping season in 2016. Corn was grown in 14 enclosures following current agronomic procedures, and was subjected to grazing by 2 densities of rabbits (44.44 rabbits per hectare and 88.89 rabbits per hectare) in 3 different growth stages: emergence (7 days after sowing [DAS]), tillering (21 DAS) and tassel (42 DAS) over 7 days (single-point damage). In addition, in one enclosure zero rabbits were kept, and in another enclosure 2 rabbits were kept continually. Rabbit grazing resulted in a significant decrease in the numbers of plants at the emergence stage, Also, the number of ears of corn per pen was significantly reduced by rabbit grazing. The emergence stage is the critical stage to control rabbits as rabbit grazing resulted in the highest losses in corn production during the early growth season. This knowledge provides farmers with a better understanding of the damage caused by rabbits and allows them to make informed decisions as to whether their crop needs to be protected from rabbits, and when rabbits should be managed.

These results highlight the need to monitor D_I before planting and in the early stages of planting (seedling stage of broccoli and emergence stage of corn). The D_T estimated in this thesis will provide the basis for making economically informed decisions on the management of rabbit damage to broccoli and corn crops. Future studies are required to verify these D_T, using free ranging rabbits in the field.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, financial support and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my higher degree by research candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

No publications

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No Publications

Manuscripts included in this thesis

No

Contributions by others to the thesis

I wish to express my sincere thanks to many people who have assisted me in this thesis. I have received invaluable support from my supervisors, Luke Leung, Peter Elsworth and Robyn Cave.

Professor Leung and Dr Elsworth designed this project and provided me this wonderful opportunity to study this invasive species and accumulate field trial experience, allowing me to study with so many wonderful people and work for Queensland Government. Also, Professor Luke, Dr Robyn and Dr Elsworth provided me so much assistances in drafting significant parts of this thesis and critically revising it so many times.

Sonya Fardell ensures that UQ's Wildlife Science postgraduate students are taken care of and ensure the wildlife welfare during the whole project. Mr Allan Lisle contributed to the analysis and interpretation of research data. Also, some student volunteers helped me with collecting data in the field.

Statement of parts of the thesis submitted to qualify for the award of another degree

None

Research Involving Human or Animal Subjects

This study was conducted under the University of Queensland Anima Ethics Approval. The numbers: DAFF/431/14, SAFS/152/15/DAFF and DAFF/SAFS/200/14. The copies of the Animal Ethics Approval Certificate are listed in appendix 10.

Acknowledgements

I sincerely thank my supervisors, Luke Leung, Peter Elsworth and Robyn Cave for their support and guidance. Thank you for providing me wonderful opportunities to study this invasive species and accumulate field experience. I especially thank Professor Luke for giving me this chance to study with so many wonderful people and work for Queensland Government. Thank you, Dr Elsworth, for giving me so much guidance to design and handle this program. Thanks Dr Cave for providing me so much assistant in crafting all aspects of this thesis.

Other staff and students I wish to acknowledge, including Sonya Fardell, a wonderful woman who ensures that UQ's Wildlife Science postgraduate students are taken care of, Mr Allan Lisle, a patient and understanding gentleman, who greatly enhanced my knowledge of statistics, and student volunteers who helped me with collecting data in the field.

Most importantly, I thank my parents, without whom I would not able to study in my ideal university and stick with my ideals. Thank you so much.

Financial support

No financial support was provided to fund this research

Keywords

Density threshold, Rabbit control, Yield loss, Simulation, Broccoli compensation, Corn

Australia and New Zealand Standard Research Classifications (ANZSRC)

ANZSRC code: 060202, Community Ecology (excl. Invasive Species Ecology), 50%

ANZSRC code: 070603 Horticultural Crop Protection (Pests, Diseases and Weeds), 40%

ANZSRC code: 140201, Agricultural Economics, 10%

Fields of Research (FoR) Classification

FoR code: 0602, Ecology, 50%

FoR code: 0701, Agriculture, land and Farm Management, 50%

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Bait	An item, usually food, used as a lure to in trapping, fishing, etc. Also refers to a poisoned lure for controlling pests.
Burrow	A single tunnel, usually used by an animal for resting, nesting and rearing of young.
D_I	Initial density
D_T	Density threshold, above which the economic benefits of control exceed the economic cost of control.
DA&F	Department of Agriculture and Fisheries
DAT	Day after transplanting
DAS	Day after sowing
Home range	An area where an animal spends its time; related to a territory.
Myxomatosis	A disease in rabbits caused by MYXV.
MYXV	Myxoma virus, which causes the disease myxomatosis in rabbits.
RGR	Relative growth rates
RHD	Rabbit haemorrhagic disease, a disease which affects rabbits, caused by RHDV.
RHDV	Rabbit haemorrhagic disease virus, a calicivirus which causes RHD.
Warren	System of underground, connecting tunnels and chambers, often with multiple entrance.
YL	Yield loss caused by rabbits

CHAPTER 1. Introduction

The European rabbit (*Oryctolagus cuniculus*) was introduced to Australia for sport hunting (McLeod, 2004), and as a protein source because of its ability to convert a wide range of vegetation into meat within a short period (Thompson and Worden, 1956). The rabbit has become one of the most abundant and widely distributed mammals in Australia, causing extensive economic losses in the agricultural and horticultural industries as well as the environment (Williams and Moore, 1995; Cooke et al., 2004; Cooke, 2012). For example, the value of lost production, caused by rabbits, is about $206 million annually (Gong et al., 2009), the cost of rabbit control is about $20 million per year (Gong et al., 2009), and the total cost throughout the whole of Australia is about $225 million per year (Gong et al., 2009).

The rabbit in Australia originated in southern France and Spain. The first domesticated populations arrived in New South Wales with the First Fleet as a source of food (Rolls, 1969), and feral rabbits in Australia were first reported in south-eastern Tasmania in 1827 (McLeod, 2004). In 1859, 24 wild European rabbits, brought from England by Thomas Austin, were released on mainland Australia, at his property near Geelong, Victoria, for sport hunting on Christmas Day (McLeod, 2004). In the 1860s, the British subspecies of the European rabbit, *Oryctolagus cuniculus*, were found almost everywhere south of the tropics and spread throughout Australia (McLeod, 2004). Around 1880, landholders began to realise the threat of rabbits to agriculture in Australia and started constructing a rabbit-proof fence to stop rabbits from spreading into northern Australia (Williams et al., 1995). However, the fence gradually failed with only one remaining section being maintained to protect South East Queensland from the spread of rabbits (Williams et al., 1995). Rabbits were first reported in south-western Queensland in 1887 (Johnson and Osmond, 2008), and by 1900 they had reached Western Australia and the Northern Territory (McLeod, 2004).

Research in 2008 has shown that the number of rabbits in Queensland might reach 14 million (Johnson and Osmond, 2008). Rabbits have ranged beyond the northern extent of the rabbit-proof fence and moved south, with the first detection of rabbits in the horticultural region being recorded in Gatton in 2009 (Watson, 2015). Since then, increasing numbers of rabbits have been reported in South East Queensland, particularly in the major vegetable-growing region, the Lockyer Valley. An increasing number of growers in this region have reported damage caused by rabbits to their vegetable crops. The Queensland Government has supported my research into creating useful scientific knowledge to manage this pest in vegetable crops.

Rabbits have recently caused serious damage to broccoli in the Lockyer Valley. The Queensland Times (2014) reported rabbit numbers in the Lockyer Valley had reached a high level, and rabbits had already destroyed some landholders' broccoli farms. Broccoli is Australia's 10th largest vegetable crop in terms of value, accounting for 3.4% of total vegetable production, with a gross value of $101.2 million in 2008–09 (AusVeg, 2010). Queensland is one of the largest broccoli producers in Australia, with 20% of national production in 2009 (AusVeg, 2010). Australia's major brassica-production area is located in Queensland's eastern Darling Downs and the Lockyer Valley (Department of Agriculture and Fisheries, 2014). The Australian Bureau of Statistics (ABS) Survey 2009 shows the Queensland broccoli industry was worth $20.52 million, with 8,732 tonnes grown on 1,556 ha (Department of Agriculture and Fisheries, 2014).

Previous studies of rabbit damage and reports from corn growers indicated rabbits would be able to cause severe damage to corn. However, most growers in the Lockyer Valley prefer to sow again after severe damage. Compared with some other summer crops, such as cotton and sorghum, corn is a relatively minor crop in terms of both production and area (Pacificseeds, 2015). However, in the Lockyer Valley, corn is an important crop. Corn (*Zea mays*) is ranked 5th in terms of production in Queensland, after wheat (*T.aestivum*), sorghum (*Sorghum bicolor*), cottonseed and barley (*Hordeum vulgare*) (Pacificseeds, 2015). In 2015, the production of corn in Queensland was 0.164 tonnes (The State of Queensland, 2017a), and the yield of corn was 5.5 tonnes per hectare (The State of Queensland, 2017b). Corn is used by a wide range of industries, such as stockfeed, starch extraction, snack foods and breakfast cereals. Corn is also grown for silage (Pacificseeds, 2015).

Many biological, physical and chemical control methods have been developed since rabbits were recognised as a serious pest in Australia (Table 1.1). However, a cost-effective rabbit management strategy based on the cost and benefit of rabbit control to manage damage caused by rabbits is still lacking (Williams and Moore, 1995).

Table 1.1 Past and current methods for controlling rabbits in Australia (Williams et al., 1995, Adams, 2017)

Biological controls	**Physical controls**	**Chemical controls**
Myxoma virus (MYXV; released in 1950)	Warren ripping Shooting	Warren fumigation
Rabbit hameorrhagic disease virus (RHDV; officially released in 1996)	Snares Removal of harbourage	Baiting (1080 & pindone)
RHDV-K5 (released in 2017)	Exclusion fencing Trapping	

From an economic viewpoint, an effective rabbit-control program would be one in which the cost of control was equal to or less than the economic benefit of implementing that control. Currently, there is limited knowledge about the economic costs and benefits of rabbit control in vegetable crops because of the lack of information about the relationship between rabbit density (D_l) and level of damage caused by rabbits. Estimating the relationship between pest density and damage is fundamental to determining the threshold pest-population density above which the economic benefits of control exceed the economic costs of control (Norton, 1976). When vegetable growers assess the economic cost and benefit of rabbit control, many factors should be taken into account, especially the value used for gross margin, and the rabbit density in the crop. Mutze et al. (2014) reported that because of the lack of simple methods to estimate the density of rabbit populations in native vegetation, even though the European rabbit has been a severe environmental pest in Australia, the reporting of density-damage relationships has been hindered. An estimate of European rabbit numbers in Australia can be made easily and quickly using two methods: spotlight transect counts and active burrow-entrance counts (Ballinger and

Morgan, 2002). Also, a new methodology has been found by Mutze et al. (2014) to estimate the rabbit density from pellet density. The cost of rabbit control will vary, depending on the control method chosen, the density and number of rabbits, and the total area that needs to be controlled (Johnson and Osmond, 2008). Approximate costs of conventional large-scale rabbit control have been estimated and are listed in Table 1.2 (Johnson and Osmond, 2008).

Table 1.2 Estimated cost of some control measures in Queensland (2008 price) (Johnson and Osmond, 2008)

Control method	***Density*** (rabbits/warrens per hectare)	***Cost*** ($ per hectare at 2008 price)
Baiting	Low (20–30 rabbits) High (70+ rabbits)	3–64
Warren destruction/ripping	N/A	3–20 (4–12 per warren)
Fumigation	Low (1–5 warrens) Medium (5–10 warrens) High (10+ warrens)	6–26 26–66 66+
Rabbit-proof fencing	N/A	4000–6000 (per kilometre)

Damage in pest management science is usually defined by two terms: economic injury level (EIL) (Higley and Pedigo, 1996) and economic threshold (ET) (Ramirez and Saunders, 1999). EIL and ET are fundamental integrated pest management (IPM) concepts. EIL is the smallest number of pests, usually insects, that will cause yield losses equal to the pest management costs (amount of injury); ET describes the lowest pest density that is correlated with economic loss at harvest (Stern, 1973; Higley and Pedigo, 1996; Sterner, 2008; Pedigo and Rice, 2014). Integrated pest management (IPM) strategies imply predictable amounts of damage, based on population size or density of the pest species. The historical focus of IPM upon insect damage is not surprising as insects have been the main pest to horticultural crops (Kogan, 1998; U.S. General Accounting Office, 2001). However, it might be difficult to use the IPM approach to manage vertebrate pests because vertebrate pests are much larger, occur at much lower densities, are more mobile and behaviorally, more flexible than invertebrates with more localised, sporadic damage (Sterner, 2008). Also, only a small portion of vertebrates is related to crop damage and even fewer is relevant to wide-area, labour-intensive, annual-indexing techniques (e.g. snap traps, pesticides) and control applications (Ramsey and Wilson, 2000; Anderson, 2001; Witmer, 2007;

Sterner, 2008). Therefore, smaller vertebrates, such as birds (e.g. black birds, gulls, cormorants) and rodents (e.g. mice, rats, ground squirrels), are the most studied species for IPM schemes for horticultural settings (Ramsey and Wilson, 2000, Peer et al., 2003, Sterner, 2008). While insects can be efficiently controlled with chemicals, vertebrates may require many diverse management techniques, such as chemical pesticides, shooting, repellents, and Sherman traps (Sterner, 2008).

There are many challenges in developing ET and EIL in open fields where vertebrate pests and their predators will readily move in and out of the study sites. Therefore, enclosure trials and pot trials are necessary for limiting these confounding factors. According to Brown and Singleton (2002), assessing the damage and yield loss (YL) caused by vertebrate pests is one of the most difficult challenges in managing the damage caused by these pests. Accurately assessing the damage and YL caused by rabbits is critically important for managing damage caused by rabbits to vegetable crops.

In the area of pest control, there are some similarities between the rabbit and the house mouse, such as they are both widespread in crops in Australia and they consume crop plants which causes serious loss in the agricultural and horticultural industries. However, the differences between them cannot be ignored. The house mouse (*Mus domesticus*) is a small mammal of the order Rodentia, one of the most important model organisms in biology and medicine. It is also one of the most studied vertebrate pests in Australia. The rabbit (*Oryctolagus cuniculus*) belongs to the Lagomorph family. The house mouse can dig up and eat newly planted seeds, cut stems, and eat developing grain (Brown, 2005); but the most significant damage always occurs at the later stages of crop growth, particularly after mice begin their breeding season in early spring (Brown and Singleton, 2001). Thus, the maturing stage of crops is the main at-risk period to house mouse damage, and the most economic damage occurs at the sowing stage. In contrast, rabbits breed all year round; they are grazers, preferring to eat the green leaves of crops rather than seeds. For this reason, an experimental design used for studying house mouse damage to crops (Kaboodvandpour and Leung, 2010) could be used in a rabbit-damage study. Enclosure trials and pot trials are necessary in the study of rabbits. By comparing the yield in enclosure trials and pot (simulated damage) trials, the damage caused by rabbits (YL) can be estimated independently.

The main objective of this study is, therefore, to determine the relationship between D_I and crop YL and to use this finding to investigate the threshold pest population density (D_T), above which the economic benefit of control exceeds the economic cost of control (Norton, 1976). This knowledge is useful for farmers to make economically informed rabbit-control decisions based on the cost and benefit of control.

This thesis aims to answer three research questions:

1. What is the relationship between damage caused by rabbits and broccoli YL?
2. How do broccoli plants compensate for damage caused by rabbits?
3. What is the effect of rabbits grazing on corn?

Chapter 2 is a literature review of the ecology and management of the introduced rabbit in Australia. This review provides background knowledge that underpins the approaches used to develop the research questions and experimental designs of current study. The thesis consists of three experimental chapters: Chapter 3, Determining density threshold for managing rabbit damage to broccoli (*Brassica oleracea* L. var. *italica* 'Anaconda'); Chapter 4, the effect of simulated rabbit damage on broccoli (*Brassica oleracea* L. var. *italica* 'Anaconda') yield; Chapter 5, assessing the effects of rabbits grazing on corn. The key findings and future directions are presented in Chapter 6.

CHAPTER 2. A review of European rabbit (*Oryctolagus cuniculus)* ecology and management in Australia

2.1 Introduction

The family *Leporidae* first appeared in North America in the late Eocene period and by the Miocene period it was found in Europe (Dawson, 1981). According to current records, during the middle Pliocene period, the genus *Oryctolagus* was first found in Spain. There are two European subspecies, *O. cuniculus cuniculus* from southern France and *O. cuniculus buxleyi* from Spain. Some studies indicate these two subspecies have been separated for more than 1 million years (Biju-Duval et al., 1991).

The wild rabbit has become one of the most abundant and widely distributed mammals in Australia, causing millions of dollars of losses in agricultural production (McLeod, 2004). Its adaptable nature, reproduction rates, and opportunistic, fast growth rate make it a very successful invasive species in Australia (Gibb, 1990). From the beginning of the 20th century, various methods have been used to control the rabbit population with the aim of reducing the significant damage caused by rabbits to the ecosystem and economy in Australia. However, most of these methods have proved to be inefficient and/or ineffective (Cox et al., 2013). Large-scale effective control of rabbits was not achieved until the introduction of selected biological control agents, such as myxoma virus and rabbit haemorrhagic disease virus (CSIRO, 2015).

In this literature review, I review the ecology of the rabbit in Australia, synthesising findings about the past and current management methods of rabbits in horticultural and agricultural crops in Australia. This information will be used to identify future research priorities for understanding the ecology of rabbits and developing more effective control of the damage caused by rabbits.

2.2 Ecology of the European rabbit

2.2.1 Current status and distribution

Rabbits in Australia were estimated to spread at the rate of 125 kilometres per year in New South Wales and, by 1866, rabbits had reached Queensland and by 1910 the Carpentaria region (Gilbert et al., 1987). In the arid watercourses and the dry southern savannah, the rate of spread was shown to be faster, than in forests, woodlands and mountains (Figure 2.1) (Fullagar, 1978, 1981). It has been said, ‘The rate of the spread of rabbit in Australia was the fastest of any colonising mammal anywhere in the world’ (Caughley, 1977).

Nowadays, rabbits are spread throughout Queensland (Figure 2.2), with high populations in the Granite Belt and the south-west; moderate populations in the Maranoa, southern Warrego and north Burrnett, and on the Atherton Tableland and south-west and north-west Darling Downs; and isolated populations in the remainder of the state (The State of Queensland, 2017c). According to P. Elsworth (pers. comm. 27 June 2017), creek lines offer protection as they are generally poorly managed by landholders, allowing long grass and dumped material to provide harbour. Natural events, such as the 2011 flood through the Lockyer Valley region, damage burrows and kill some rabbits but also force movement further along catchment areas.

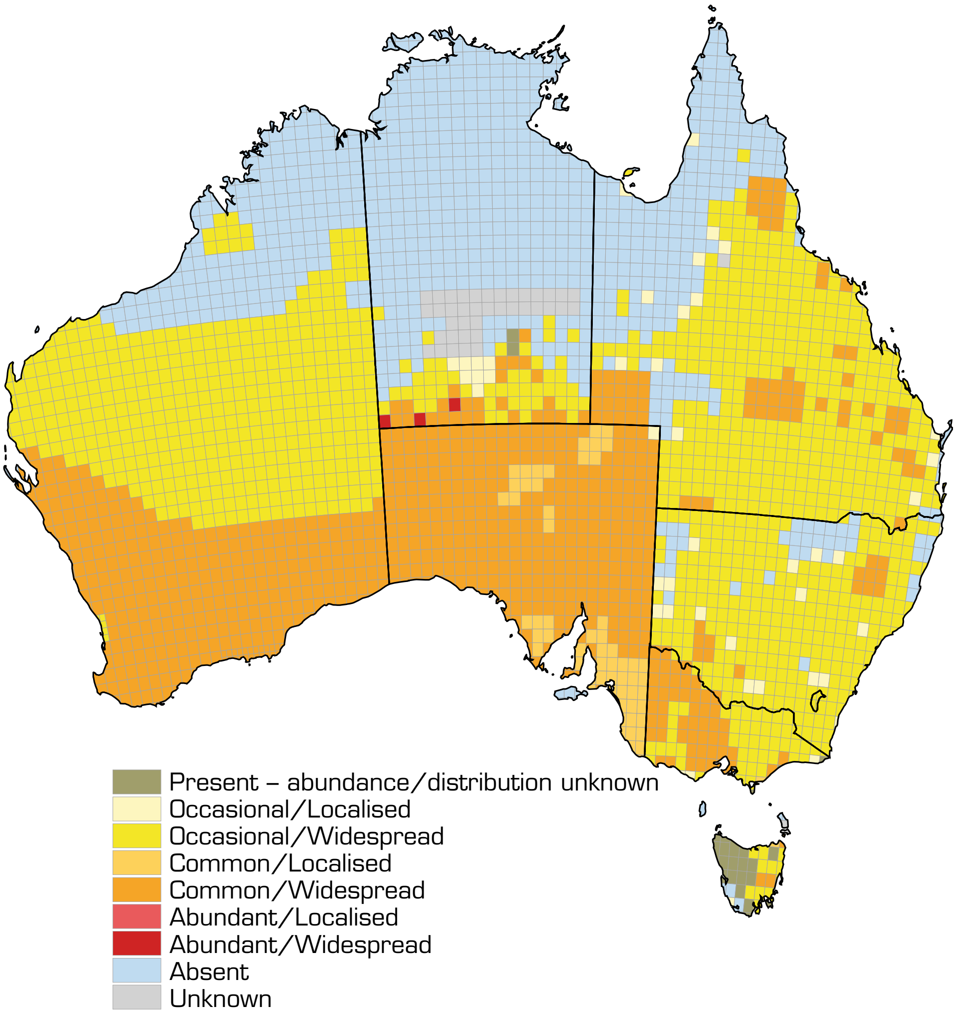

Figure 2.1 Occurrence, distribution and abundance of rabbits throughout Australia (National Land & Water Resources Audit and Invasive Animals Cooperative Research Centre, 2008).

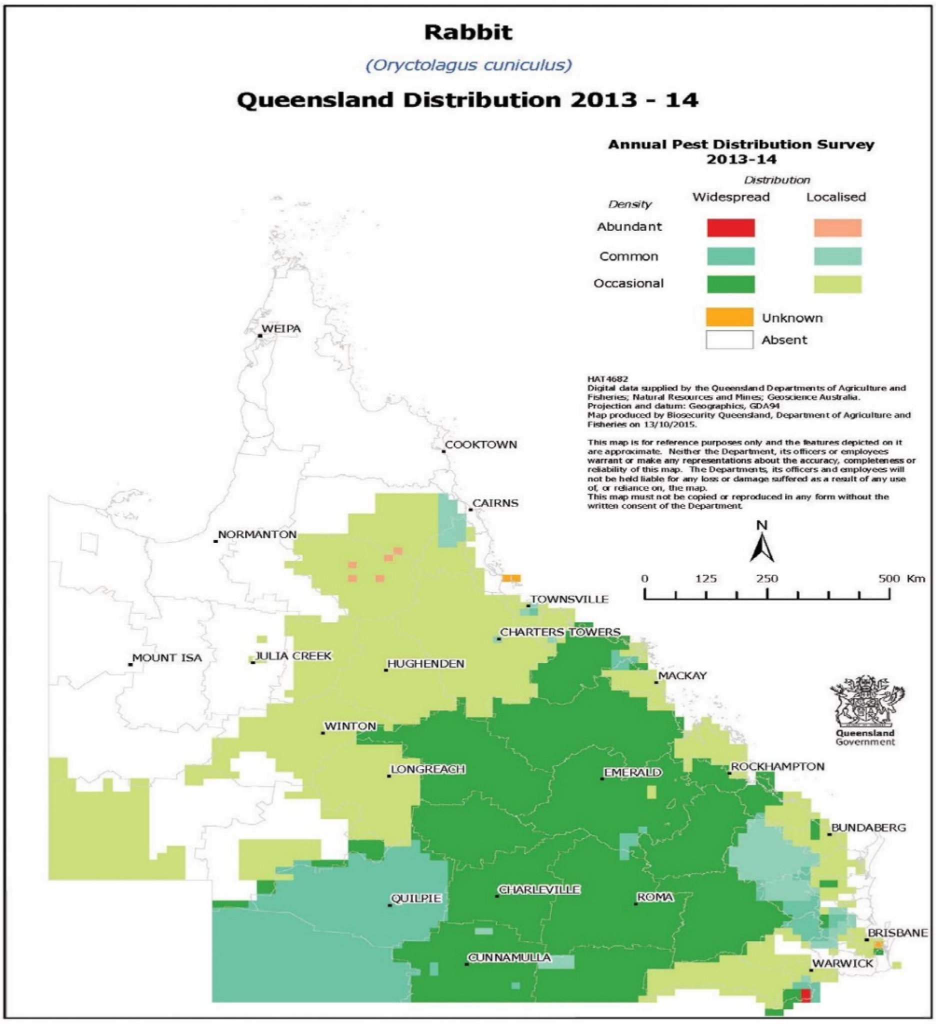

Figure 2.2 Distribution of rabbits in Queensland (The State of Queensland, 2017c).

The density of rabbits is usually estimated by counting the number of rabbits directly in an area, and is indexed by the number of warrens and entrances of warrens, and indirectly estimated by various rabbit-signs (Mitchell and Balogh, 2007). However, many factors—such as the weather, time of day, season, vegetation type, length of pasture, observer, and methodology—will affect the accuracy of estimates of D_l and these estimations usually have large variances (Cruz et al., 2013). The D_l in Australia prior to the introduction of myxomatosis was not known; however, after this, D_l was estimated to range from 2 to 97 rabbits per hectare, with the average D_l being 3 rabbits per hectare (Wood et al., 1987). Although D_l in Australia is difficult to estimate precisely, some reports rank the D_I at 3 levels: low (1–4 per hectare), medium (6–30 per hectare) and high (more than 30 per hectare) (Williams et al., 1995).

The density and distribution of the wild rabbit apparently differs between habitats. In most habitats, rabbits will live nearby or even within herb fields as there is an abundant food supply (Jarman and Johnson, 1977). The wild rabbit is known to live close to the sand along drainage channels in temperate subtropical Queensland (114 warrens per kilometre) (Parker et al., 1976). However, it is difficult to show the rabbit distribution pattern. For habitats in the southern agricultural regions, even in the most optimal environments, D_I was only 3.5 warrens per hectare and also discontinuously distributed (Myers and Poole, 1962). Parker et al. (1976) indicated that the southern agricultural region was a low-lying region that is frequently flooded causing a low D_I.

According to Parer (1977), soil type is one of the most important factors that influences the local and regional population and distribution of rabbits (Parer and Libke, 1985; Parker et al., 1976). Rabbits are rarely found inhabiting areas with black cracking soils; they always actively occur in regions with well-drained soils (Williams et al., 1995). According to the Department of Agriculture and Fisheries (2018): Black alluvial clays and clay loams are the most productive soils in the Lockyer Valley, the soils associated with the upper catchment tributaries and the levee banks of the Lockyer Creek are generally well drained with a loam texture … Almost all the black alluvial soils in the region are suitable for irrigation and vegetable production. This is one of the reasons why the density of rabbits in the Lockyer Valley region is very high.

Rabbits can change their home-range size, shape, and location in response to different environmental conditions. Rabbits dig warrens for protection, breeding, and reducing exposure to myxoma virus (Myers and Poole, 1961; Mykytowycz and Gambale, 1965; Dunsmore, 1971; Parer, 1982). Rabbits construct large warrens up to 3 metres deep and 45 metres long. Daily movements of rabbits are generally within 150 to 200 metres of the warren, but the distance can increase during droughts (up to 1,500 metres has been observed) or decrease during the breeding season (Verbeek, 2018).

Except in sandy soil environments, typically, rabbits will not dig new warrens (Parer, 1977). When they enter a new area, a rabbit will often live in either a shallow depression in the ground, a stop (a short burrow about one metre long), under fallen timber, or in depressions in long vegetation, which is named a squat (Williams et al., 1995). Inside a stop, the entrance is always covered by soil, which makes it difficult to be found. A warren is an extensive stop, usually much deeper, with separate tunnels that are used for successive litters (Mykytowycz, 1960).

The deep, elevated sandy soil nearby a floodplain is the best location for warrens (Myers and Parker, 1975, Rogers and Myers, 1979, Cooke et al., 2004). The warren provides protection from predators and extreme environmental conditions, which makes the European rabbit the only rabbit species that can survive in open grassland (Myers and Poole, 1962). It is easy to detect a warren because the warren is usually surrounded by a variety of vegetation due to rabbit activity that disturbs the soil and native vegetation (Poczopko, 1969). Soil permeability to water, soil hardness and soil depth are the main factors influencing the locale of warrens and the regional distribution of rabbits (Poczopko, 1969). Typically, human activity and soil type will affect the size of a warren (Cowan and Garson, 1985, Kolb, 1985), which can be very extensive.

2.2.2 General ecology

Rabbits from different geographical regions in Australia vary in development rate, physiological indices and body size (34–50 centimetres) (Stodart, 1965, Casperson, 1968, Myers et al., 1971). These variations are caused by the differences in climate and indices of nutrition, which are affected by light, temperature, moisture and plant performance in different climatic regions (Thompson and King, 1994).

2.2.3 Diet and nutrition

The wild rabbit is a mixed-feeder—their diet includes roots, tree bark, buds and leaves in their diet—but grasses are their primary choice (Pascual et al., 2003). Additionally, grains, root vegetables such as carrot, leafy vegetables such as cabbage and lettuce, and some other vegetables are included in their diet (Pascual et al., 2003). The diet and nutrition requirements of the rabbit in Australia are influenced by the density of rabbits, rainfall, soil fertility, and growth of pasture, which is affected by seasons (Rueda et al., 2008). Limited food, drought, imbalance of minerals, and high temperatures also influence rabbit nutrition (Rueda et al., 2008). Cooke (1974) estimated the basic requirement of protein for wild rabbits to support their metabolism is about 12%. When food and water are limited, rabbits will eat termites, tree roots, fallen tree leaves and bark (Myers and Bults, 1977; Cooke, 1982). The rabbit will extend the range of its habitat during dry periods and can dig roots or eat leaves and the bark of perennials for reserves of water and protein (Cooke, 1984).

To satisfy their own nutritional requirements, young rabbits will quickly learn how to detect the required sources of minerals, water and protein (Myers and Poole, 1963). For example, in a sodium-deficient zone, the rabbit will search for and take sodium-rich seed heads (Blair-West et al., 1968). However, in an arid environment, the rabbit will avoid eating plants rich in sodium even though they are rich in water and protein (Pech et al., 1992). Also, rabbits need to consume their own faeces to receive more nutrition from what they eat, which is a unique digestive process of rabbits, guinea pigs, most of the other rodents and some other mammals. This process is known as 'pseudo-rumination', 'hindgut fermentation', 'coprophagy' or 'caecotrophy' (Taylor, 1941, Tynes, 2001). Caecotrophy is a vital process for herbivorous mammals with a rapid metabolic rate and small body size (Halls, 2008). It allows rabbits to consume poor quality, high-fibre diets and obtain necessary nutrients, providing proteins, essential amino acids and B vitamins from bacterial sources (Halls, 2008, Blas and Wiseman, 2010).

2.2.4 Reproduction and survival

The reproductive cycle of rabbits in Australia is influenced by nutrition and length of daylight (Boyd, 1986; Bell and Webb, 1991). Generally, the high point of breeding is spring, and the lowest is autumn. Previous studies have demonstrated that rabbits in Australia will breed from the period when the soil becomes moist and pastures start growing, until the point that the soil moisture limits the growth of pastures and then they dry out (Myers et al., 1989). The female rabbit can mate within hours after giving birth, and up to 100% can be pregnant in successive months, although most will only breed 3 to 4 times per year (Dunsmore, 1974). The gestation period ranges from 29 to 35 days.

Reproduction behaviour is influenced by the environment, which affects the success and frequency of reproduction (Myers and Poole, 1962; Wood, 1980; Cooke, 1981, Wheeler and King, 1985; Myers et al., 1989; Moseby et al., 2005). In different environments, the length of time a young rabbit takes to mature differs (Dawson and Ellis, 1994). In mature females, the number of eggs fertilised and shed increases with age, but this also varies with environmental conditions (Wheeler and King, 1985; Gilbert et al., 1987). Furthermore, a high temperature is a limiting factor for rabbit breeding (Finzi, 1994; Cooke, 1997; Tablado et al., 2009). Territorial behaviour of rabbits is related to their reproduction; the male will keep females from other males and the female will fight against other females to protect their burrows (Parer, 1977; Christine, 1979).

2.3 The rabbit in Australia

2.3.1 Pest issues

2.3.1.1 Economic impacts

The economic impact of rabbits has been quantified in Australia for pastoral, grazing and wool production industries. According to Williams and Moore (1995), the rabbit has become one of the most abundant and widely distributed mammals in Australia, resulting in tremendous economic loss in the agricultural and horticultural industries. Prior to the release of RHDV, rabbit-related production losses in the Australia wool industry were estimated to be $130 million per year (Gong et al., 2009). Since the release of RHDV these costs have declined (Saunders et al., 2002). To temperate-region wool producers, the cost of rabbits in the absence of RHDV was calculated to be between $40 and 73 million per annum (Vere et al., 2005). The value of lost production, caused by rabbits, for pastoral districts of South Australia prior to RHDV was about $20 million annually; and for agricultural production throughout the whole of Australia it was about $113.11 million per year (Williams et al., 1995).

Rabbits feed on emerging crops, and up to 100% of YL have been recorded on the fringes of paddocks in Western Australia (McLeod, 2004). The most recent economic evaluation placed rabbits as the highest vertebrate-pest cost to Australian agriculture, including horticulture, causing about $206.01 million damage per year (Gong et al., 2009). According to Williams and Moore (1995) and Croft et al. (2002), the main economic impact of rabbits is to reduce the sale weight of calves and lambs, and to reduce the amount of wool produced per animal (Gong et al., 2009). The annual losses to economic surplus caused by rabbits to beef industry is $161.05 million, lamb industry is $13.43 million, and wool industry is $31.54 million (Gong et al., 2009).

Overall, rabbits are economically the most important agricultural pest in Australia, causing more than $200 million in pre-harvest production losses each year (Cooke et al., 2013). The releases of biological control agents, myxomatosis and calicivirus, to control rabbits have provided cumulative benefits of up to $70 billion to the agricultural industry over the past 60 years (Cooke et al., 2013).

2.3.1.2 Environmental impacts

Information on the impact of introducing rabbits into Australia mainly comes from circumstantial observations and reports (Mallick and Driessen, 2009). According to these reports, rabbits cause many negative impacts on geological features, native flora and fauna, nutrient recycling systems and natural landscape value (Johnson and Osmond, 2008). The most serious problem with the wild rabbit is the stripping and destroying of perennial shrubs and seedling trees (Anonymous, 1901; Jessup, 1951; Ratcliffe, 1959). As Johnson and Baird (1970) reported, the regeneration of *Acacia* spp. was prevented and bluebush (*Mariana sedifolia*) was damaged wherever rabbits occurred (Johnson and Baird, 1970). In addition, when the rabbits were introduced onto coastal islands, the vegetation of these areas changed, which caused heavy soil erosion, such as on Macquarie Island (Williams et al., 1995). On Macquarie Island, the grazing impacts of rabbits also affect the nesting behaviour of many seabirds, including grey, blue, and white-headed petrels (Johnson and Osmond, 2008). Rabbits eat and damage leaves and flowers, destroy seedlings and root systems, and then cause erosion of the steep peat-covered slopes (Johnson and Osmond, 2008). By transporting seeds in their fur, rabbits on Macquarie Island also change the distribution of plant communities (Johnson and Osmond, 2008). Furthermore, it has been demonstrated that the invading rabbit plays an important role in the extinction of small and medium-sized mammals, such as the boodie (*Bettongia lesueur*) and the sticknest rat (*Leporillus spp.*) (Johnson and Osmond, 2008). The invading rabbit is also contributing to the disappearance of the bilby (*Macrotis lagotis*), which has been officially classified as endangered in Queensland and vulnerable to extinction in other areas (Johnson and Osmond, 2008).

2.3.2 Past and current management

Since 1880, the government and landholders began to realise the threat of the rabbit to agricultural and horticultural crops. They tried to control the spread of rabbits by constructing thousands of miles of rabbit-proof fences, which by 1890 had done little to solve the issue in south-eastern Australia and the rabbit population spread rapidly. At this time, poison was used to control the population but with little impact (Williams et al., 1995). Some farmers tried to net the boundaries of their properties, remove the rabbit harbour and dig out their warrens with shovels and picks, and they regularly inspected the fence and hunted down all rabbits when they appeared. These methods were successful in controlling the damage caused by the rabbits for a short period of time and in limited areas (Williams et al., 1995). However, at this time, widespread control of rabbits was not possible.

After CSIRO introduced myxomatosis in 1950, the number of rabbits were effectively controlled in the higher rainfall zones within a few years (Kerr et al., 2015). In 1995, the outbreak of rabbit haemorrhagic disease (RHD), also known as calicivirus disease, killed 14 million wild rabbits within 9 months (Williams et al., 1995). Both myxomatosis and RHD have reduced rabbit populations below 10% of their former level and this has allowed other techniques to be more successful—such aswarren ripping in arid zones (Williams et al., 1995). Another method to control the rabbit population was the use of the poison compound 1080 (Williams et al., 1995). While there are some species that are not affected by 1080 (native species from Western Australia where 1080 naturally occurs in some native plants), others are sensitive to its effects, such as rabbits, dogs, foxes, possums, cattle, sheep, and humans (Cooke, 2012). Furthermore, studies have shown that the innate resistance of rabbits to both myxomatosis and 1080 is increasing (Ross and Sanders, 1977; Twigg et al., 2002; Marchandeau et al., 2014). In addition, only limited methods are available that can be effectively used to reduce rabbits in low-rainfall zones. Recently, destruction of warrens to control rabbits in arid zones has been shown to be successful (Berman et al., 2011). RHDV-K5, a new strain of calicivirus disease, was scheduled to be released by CSIRO in Autumn 2017 to add to the biological control of rabbits (Adams, 2016). In Australia, government authorities and other researchers have attempted to establish economic studies to control rabbits (Berman et al., 2011). Economic studies provide information for land managers to better understand the economic impacts of pest animals and the control options available to them. This allows the managers to make informed decisions on the economic benefits of pest animal (in this case, rabbits) control.

The complete eradication of rabbits from the Australia mainland is not a realistic short-term goal; although, eradication is possible in some fenced areas (Johnson and Osmond, 2008). In 2004, the Macquarie Island Pest Eradication Project was developed by the Australian and Tasmanian governments to remove rabbits and rodents from Macquarie Island (Parks and Wildlife Service, 2014). To achieve eradication, a combination of techniques is required and a series of conditions are needed, such as entire populations of the target species must be under control and prevented from re-invasion (Bomford and O'Brien, 1995; Johnson and Osmond, 2008; Coyne, 2010; Parks and Wildlife Service, 2014). Therefore, an eradication plan is usually suitable for a small islands and often more cost-effective than long-term sustained control (Parks and Wildlife Service, 2014). In Australia, there have been 22 successful rabbit eradication programs on islands, including Phillip Island, Cabbage Tree Island, Montague Island, Broughton Island and Macquarie Island. In 2014, the steering committee announced there had been no confirmed sightings of rabbits on these islands since December 2011, after the Macquarie Island Pest Eradication Project was developed by the Australian and Tasmanian governments in June 2007 (Parks and Wildlife Service, 2014).

2.3.3 Economics of rabbit management

An economically efficient rabbit-control program would be one in which the economic cost of control is less than the economic benefits of control. Estimating the relationship between pest damage and pest density is fundamental to determining the threshold pest population density (D_T), above which the economic benefit of control exceeds cost of control (Norton, 1976; Kaboodvandpour and Leung, 2012). When land managers assess the economic costs and benefits of rabbit control, many factors should be considered, such as D_I and cost of control. It is difficult to estimate D_I, and the results of any such efforts have wide standard errors. Typically, the number of active warren entrances, are used to index the number of rabbits (Parer, 1982). The cost of rabbit control depends on the methods used and whether farmers use their own equipment and labour. Approximate costs of conventional rabbit control on a large scale are: about $6–8 per hectacre for poisoning; $3–20 per hectacre for warren ripping; $10–20 per hectacre for fumigation; and $30–60 per hectacre for using explosives to destroy burrows (Williams et al., 1995).

It is important to consider the economic effects of pest control. Damage caused by pests is usually defined by two terms: economic injury level (EIL) (Higley and Pedigo, 1996) and economic threshold (ET) (Ramirez and Saunders, 1999). Until now, most research into these two parameters has been focused on insect pests and their control. According to Brown et al. (2007)—when establishing the damage to crops and the economic impacts—assessing the damage and YL, caused by rodents, is one of the most difficult challenges. For rabbits, accurately assessing their damage and subsequent YL is essential for estimating the relationship between D_I and economic impact and damage to crops.

In this study, I therefore aim to estimate the relationship between D_I and crop YL through determining D_T, above which the economic benefit of control exceeds the economic cost of control (Norton, 1976). The results from my study will assist farmers in making appropriate decisions regarding rabbit management strategies, when they are planting broccoli and corn.

2.4 Effect of herbivory on plant growth and development

In many cases herbivores are considered to be detrimental to plants (Belsky, 1986, Bigger and Marvier, 1998, Crawley, 2009), but some plants are able to tolerate biotic and physical damage and stresses (Fornoni, 2011; Stowe et al., 2000). Some research has indicated that herbivores may stimulate plant growth and increase plant fitness (Owen and Wiegert, 1976; Dyer et al., 1982; McNaughton, 1983; Maschinski and Whitham, 1989; Vail, 1994). Plant compensation is defined generally as a positive response of plants to injury. Injury means the physical harm to a commodity caused by the activity of a pest, such as eating leaves, tunneling through stalks, and eating grain (Hunt et al., 2009). In many conditions, it is difficult to distinguish under-compensation from no compensation; both are viewed more simply as a negative effect of herbivory. Overcompensation is observed in some plants such as soybean, where a small amount of injury actually increases yield slightly (Hunt et al., 2009).

Maschinski and Whitham (1989), suggested that overcompensation was most likely where water and nutrient resources were abundant and competition low, such as plants in cultivation in greenhouse studies; and they further suggested that late-season herbivory is not likely to result in overcompensation under any circumstances. However, Lennartsson et al. (1997), suggested only late-flowering plants overcompensated in their greenhouse trial (*G. campestris*.), and this trait was found to be heritable.

However, both compensation and overcompensation are not inherent in all species under any environmental conditions (Gavloski and Lamb, 2000a; Gavloski and Lamb, 2000a; Gavloski and Lamb; 2000b, Gao et al.; 2008, Garrido et al., 2012). Plant response to herbivory is specific to species, and compensation is specific to herbivory type and intensity (McNaughton, 1979; Paige and Whitham, 1987; Poveda et al., 2010). Hawkes and Sullivan (2001) suggested that dicotyledonous herbs and woody plants were able to increase their relative growth rate and recover significantly better from herbivory in low-resource conditions, while monocotyledons were the only group that grew more after herbivory in high-resource conditions.

The relationship between different levels of injury and the yield response of a given commodity can be shown using a damage curve (for example, see Figure 2.4).

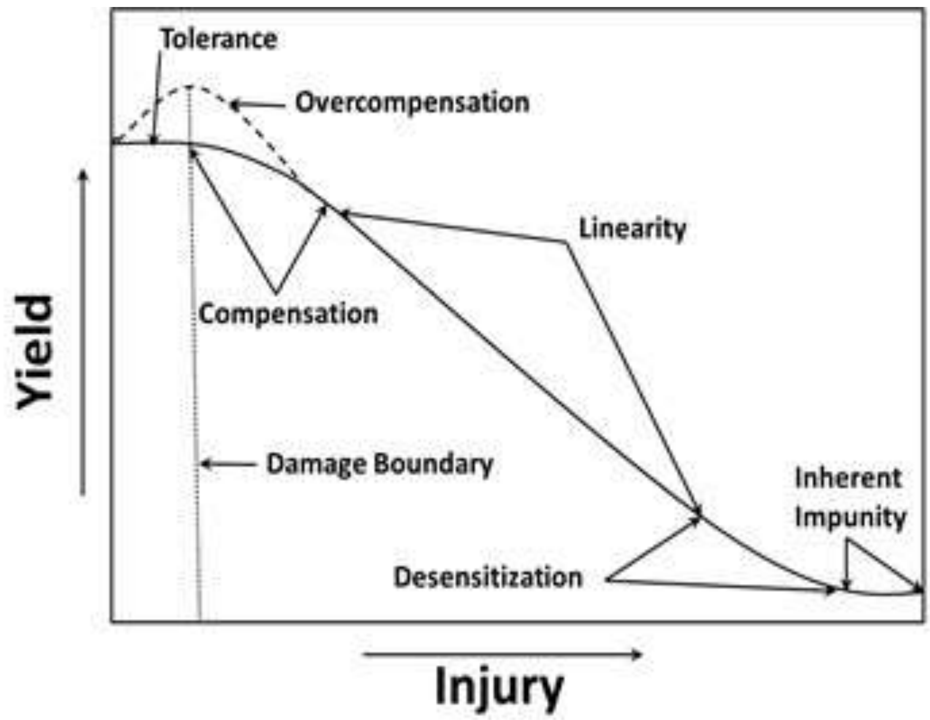

Figure 2.3 The damage curve and its components (Hunt et al., 2009).

Tolerance is when plants can sustain some injury without any effect on yield (Hunt et al., 2009). Overcompensation is observed in some plants, where a small amount of injury increases yield slightly (Hunt et al., 2009). The damage boundary is the point at which YL caused by injury is detectable (Hunt et al., 2009). Compensation is where there is increasing YL per unit of injury (Hunt et al., 2009). Desensitisation is where there is decreasing YL per unit of injury (Hunt et al., 2009). And inherent impunity is where there is no more damage per unit of injury (Hunt et al., 2009). There are a number of factors that will affect the relationship between injury and YL, including the type of injury, the timing of injury, the intensity of injury, the location of injury, and various environmental factors. Most YL research has been conducted on insect populations that corresponds to the linear portion of the damage curve (Hunt et al., 2009).

2.5 General conclusions

The introduced European rabbit (*Oryctolagus cuniculus*) is one of the most widely spread and abundant mammals in Australia. Rabbits in Australia usually live in groups underground in warrens. Rabbits require food with high-protein and high-water content to survive and reproduce. Rabbits have a high reproductive potential; generally, a female rabbit can produce up to 40 young a year. However, the high rate of production does not correlate with a high D_I as only less than 10% of young will survive past their first year (Gibb et al., 1985). The warren is the key for rabbits to successfully live and multiply in Australia as it provides protection from climatic extremes and predators.

Most evidence indicates that rabbits are one of the most serious vertebrate pests in Australia, affecting the pastoral, horticultural and agricultural industries, and the environment. Over the last 30 years, a range of rabbit-control programs have been provided by the government and land managers in Australia, such as warren destruction, poisoning, rabbit-proof fencing, shooting or trapping and biological controls, including diseases, parasites or predators. In addition, many studies about rabbits and rabbit control have been presented; about 550 references could be searched in the national guidelines for managing rabbits. However, the majority of the research focuses on the economic and environmental impacts of rabbits in Australia generally. Moreover, little information is available on rabbit damage for different crop species and the relationship between D_I and YL. Furthermore, few studies focus on the cost–benefit of rabbit management in farmlands, even though some studies indicate that rabbit management would be highly profitable. For these reasons, it is difficult for land managers to adopt the most appropriate rabbit management strategies to reduce potential YL.

Therefore, in order to reduce rabbit damage to sufficient levels, this current study aims to estimate the levels of rabbit damage at different crop-development stages, establish the relationship between D_I and population YL, and suggest appropriate rabbit management programs by assessing the D_T and economic value of rabbit control.

CHAPTER 3. Determining density threshold for managing rabbit damage to broccoli (*Brassica oleracea* L. var. *italica* 'Anaconda')

Abstract

The introduced rabbit is a major pest in horticultural industries in Australia. Estimating the relationship between pest damage and pest density is fundamental to determining the threshold pest population density (D_T), above which the economic benefit of control exceeds the cost of control. A manipulative replicated experiment was conducted to determine D_T for managing yield loss (YL) caused by rabbit density (D_I) introduced at the start of two crop development stages of broccoli. The experiment was conducted in predator and rabbit-proof enclosures on The University of Queensland, Gatton campus over the winter cropping season in 2014 and 2015. For the 2014 experiment, rabbit damage to broccoli was measured by releasing rabbits at a density equivalent to 30 rabbits per hectare into two enclosures (replicates) for 21 days at the following stages: seedling (2 weeks after transplanting), establishment (4 weeks after transplanting) and heading (6 weeks after transplanting). The experimental rabbits were not subjected to any control. Rabbits removed 10%, 70% and 100% of plants at the heading stage, establishment stage and seedling stage, respectively. In the 2015 experiment, rabbits at densities equivalent to 3.75, 7.5, 15 and 30 rabbit per hectare were introduced into broccoli at the seedling and establishment stages for 24 days. There were 2 replicates for each group. When rabbits were introduced at the seedling stage, the relationship between D_I and YL was linear, with YL increasing with D_I. When rabbits were introduced at the establishment stage, there was no significant relationship between D_I and YL. D_T would vary depending on the effectiveness of the control method in reducing D_I and the cost of control as a percentage of the farm-gate value of broccoli. For example, D_T would be 6.54 rabbit per hectare for triggering RABBAIT® Pindone Oat baiting if this method was effective in reducing D_I by 94% and if the cost of baiting was 1.01% of the farm-gate value of broccoli. These results suggest that D_I should be monitored before and at the seedling stage, and that the local rabbit population should be controlled if its density exceeds D_T, based on the known farm-gate value of the crop. Rabbits should ideally be monitored at least once—well before the seedling stage, so that about a week before planting, D_I can be forecast by the trend in monitored densities.

3.1 Introduction

Estimating the relationship between pest damage and pest density is fundamental to determining the threshold pest population density (D_T), above which the economic benefits of control exceeds the costs of control (Norton, 1976). Although D_T has been a proven concept for economic management of many invertebrate pests and weeds (Doyle, 1991, Nabirye et al., 2003), only a few studies have estimated the relationship between vertebrate pest density and damage (e.g. Feare, 1974; Wilson et al., 1989; Choquenot et al., 1997; Kaboodvandpour and Leung, 2012).

The present study focused on damage to vegetable crops caused by rabbits because the cost of this damage is much higher than that for damage to cereal crops and pasture caused by rabbits (Johnson and Osmond, 2008). Overall, rabbits are economically the most important agricultural pest in Australia, causing more than $200 million in pre-harvest production losses each year (Cooke et al., 2013). Rabbits have recently caused damage to broccoli and other vegetable crops in the Lockyer Valley. The Queensland Times (Gould, 2014) reported rabbit numbers in the Lockyer Valley had reached a high level, and rabbits had already destroyed some landholders' broccoli farms. In addition, even a small amount of damage to a plant means the whole broccoli head is unmarketable. Broccoli is Australia's 10th largest vegetable crop in terms of value, accounting for 3.4% of total vegetable production, with a gross value of $101.2 million in 2008–09 (AusVeg, 2010). Australia's major brassica production area is located in Queensland's Eastern Darling Down and the Lockyer Valley (Department of Agriculture and Fisheries, 2014), and Queensland is one of the largest broccoli producers in Australia, responsible for 20% of the national production in 2009 (AusVeg, 2010). The Queensland's broccoli industry is worth $20.52 million, with 8,732 tonnes grown on 1,556 hectares (Department of Agriculture and Fisheries, 2014).

D_I were estimated to range from 2 to 30 rabbits per hectare in Queensland in the 1990s (Williams et al., 1995). However, the full range of damage to broccoli caused by rabbits is not available in published reports. Even if these data were available, it is still impossible to develop density/damage relationships. This is because of difficulties in obtaining reliable yield loss data due to large variations between sites and over time (Krebs et al., 1994; Brown and Singleton, 2002).

Determining whether the economic benefits of control will occur is important for defining D_T. Before the vegetable crops are planted, the rabbit population may decline or even collapse due to insufficient food supply or other factors such as biological virus outbreaks (P Elsworth 2018, pers. comm., 17 August). Therefore, vegetable growers will be reluctant to control rabbits if D_I is not known to exceed D_T before planting. D_T can be estimated based on the relationship between the D_I introduced at a specific crop growth stage and the YL caused by this single-point damage.

There are several published reports on the relationship between pest abundance and damage, some of which demonstrate the relationship between pest damage and initial pest abundance (Norbury et al., 2015). According to Hone (2007), there were several relationships between pest damage and constant pest densities—such as linear, accelerating, decelerating or unknown—which might be affected by the social bebaviour of pests. A positive decelerating relationship between wheat YL caused by mice and mouse density was reported by Kaboodvandpour and Leung (2008). It has been reported that blackbird damage to rice also leads to a positive decelerating relationship between pest density and yield loss (Wilson et al., 1989).

The present study aimed to determine D_T by estimating the relationship between D_I and YL in broccoli. This knowledge would enable broccoli growers to make decisions to control rabbits based on D_I in their crop.

3.2 Materials and methods

3.2.1 Experimental approach and study site

The experiment was conducted by modelling D_T for managing rabbit damage to broccoli. For 24 days, 4 known densities of rabbits per hectare (30, 15, 7.5 and 3.75) were released to seedling-stage and establishment-stage broccoli crops (*Brassica oleracea* L. var. *italica ‘Anaconda’*), which were enclosed by rabbit-proof fences (five metres high). YL was calculated by measuring and comparing yields of broccoli in rabbit-exclusion and at-risk plots. In addition, to estimate the full range of damage caused by rabbits to broccoli, a high D_I (30 rabbits per hectare) was introduced into 3 pens of broccoli that were at different stages: seedling, establishment and heading. The vegetative damage caused by rabbits and YL was measured by comparing the total leaf area of a plant and the weight of the broccoli head of the paired rabbit-exclusion (control) and at-risk plots. The vegetable crops were grown with standard agronomic practice in a typical crop field to emulate the habitat condition of field vegetable crops (e.g. alternative food supply for rabbits). The experiment was conducted in rabbit-proof pens at UQ, Gatton campus wildlife enclosures (-27°54´ S, 152°34´ E) over the autumn–winter cropping season in 2014 and 2015.

The experiment was conducted from August to December in 2014, and from May to September in 2015. The average weekly temperature ranged from 19.9 ºC to 34.9 ºC in 2014, and from -0.3 ºC to 30.1 ºC in 2015. The soil at the study site is a self-mulching, cracking alluvial soil, which is similar to but sandier than the black soil typically used for field crops in the Lockyer Valley.

3.2.2 Experimental animals

Sixteen rabbits were trapped (using cage traps baited with broccoli and carrot) from farms around the UQ wildlife enclosures. Trapped rabbits were housed in a holding pen (15 metres × 15 metres) for acclimatisation for about two weeks. Four artificial warrens were provided, also mixed vegetables, in addition to commercial rabbit pellets and clean water. The rabbits ranged from 1500 to 2500 grams in body weight.

Only male rabbits were used in experiments. Rabbits were randomly assigned to the experimental pens after stratification to ensure the body weight and health conditions were similar across pens. Experimental animals were marked by ear tags (Ohrmarken, model 73850, made by Hauptner, Zurich) for individual identification. All animals appeared to be healthy when introduced to and trapped in the pens. This study was conducted under The University of Queensland Animal Ethics Approval numbers: SAFS/152/15/DAFF and DAFF/SAFS/200/14.

3.2.3 YL assessment

Density of rabbits

Due to the size of the pens (15 metres x 15 metres) is very small, the density of rabbits would be high even if only one rabbit was introduced for the entire duration of the trial (44.44 rabbits per hectare per day). To reduce the pressure on the crops, rabbits were transferred between experimental pens and resting pens. For the experiment conducted in 2014, two replicates of high D_I (30 rabbits per hectare) and three stages of the crop were used: seedling (2 weeks after transplanting), establishment (4 weeks after transplanting), and heading (6 weeks after transplanting). Each day 2 rabbits were moved from one crop stage to the next so that each stage was visited 7 times over 21 days. This equated to a D_I of 30 rabbits per hectare.

For the experiment conducted in 2015, 4 densities of rabbits were introduced at the seedling stage and establishment stage by varying the number of rabbits and the number of days the rabbits had access to the crops. Within 24 days, 2 rabbits had 8 days access (30 rabbits per hectare), 1 rabbit had 8 days access (15 rabbits per hectare), 1 rabbit had 4 days access (7.5 rabbits per hectare) and 1 rabbit had 2 days access (3.25 rabbits per hectare). Each group was given access to seedling- and establishment-stage broccoli for those total numbers of days, and 2 replicates were used for each introduced density. In addition, within the 24-day period, rabbits were rested in separate grassed pens (10 metres x 5 metres) on the days when they did not have access to a crop.

Range of damage caused by rabbits

In 2014, 6 pens (15 metres × 15 metres) were prepared to provide 2 replicates of each plant growth stage: seedling, establishment, and heading (2, 4 and 6 weeks after transplanting). Each replicate was planted 2 weeks apart so that the 3 stages could be accessed by the rabbits on consecutive days to reduce variability associated with weather during the experimental phase. Within each pen, seedlings were transplanted into 10 prepared beds with 46 plants per bed. Each bed was approximately 1.20 metres wide and 13.0 metres long. The resulting density was 29,000 plants per hectare (typical brassica planting densities in Queensland range from 26,000 to 57,000 plants per hectare (Heisswolf et al., 2004)).

Four rabbit-exclusion plots were randomly located in each pen (Fig. 3.1) to allow some plants to act as controls. This sample size was used to increase the precision of estimating rabbit damage. The plots were located at least 1 metre from the edge of the planted area to avoid potential edge effects, and each plot was fenced off with wire mesh. Each rabbit-exclusion plot was paired with 2 at-risk plots. Each plot was 120 centimetres long × 100 centimetres wide × 40 centimetres high in dimension, and contained 6 plants. The plants inside the rabbit-exclusion plot grew so that they touched the wire mesh, which may have restricted their growth. The planting area was 13 metres x 13 metres in the pen, allowing the remaining grassed perimeter to provide an abundant alternative food source for the rabbits. A high D_I (equating to 30 rabbits per hectare) was introduced to the broccoli crop at each of the three growth stages for 7 days over a period of 21 days. The density used in this study was lower than the maximum estimated D_I in the field in Queensland. Damage was assessed by measuring and comparing damaged leaves of the paired rabbit-exclusion plots and at-risk plots immediately after the rabbits were removed from the pens.

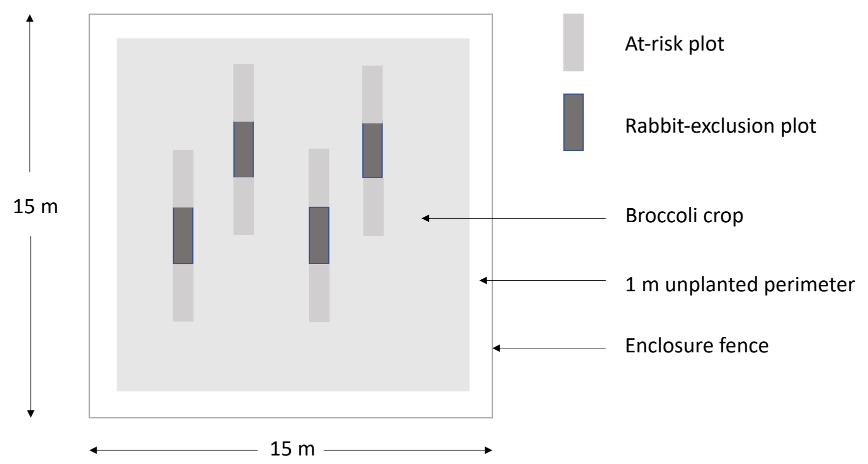

Figure 3.1 The setup of the enclosure showing the locations of rabbit-exclusion and at-risk plots in 2014, and the area planted with broccoli. Broccoli was planted 1 metre from the fence of the enclosure.

The mean damage percentage of broccoli at the heading stage was estimated using leaf area through the grid counting method. Each leaf was placed on a grid paper, outlines of the leaf were drawn by pencil on the grid paper, and the leaf area was measured by counting the grids covered by leaf (Chaudhary et al., 2012). The area that the leaf occupied was the undamaged portion (LA), and the area of damage was measured (DLA) by extending the outline of LA to depict a full, undamaged, leaf. The number of leaves was represented by ‘n’. According to LA and DLA, the mean damage percentage to the crop was calculated (Equation 1).

$$Mean\ damage\ percentage\ of\ broccoli = \frac{1}{n}\sum\left(\frac{LAn}{LAn+DLAn}\right)\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

The leaf area for early development stages was not calculated due to the extensive rabbit damage, whereby only a small number of plants remained. Instead, the damage percentage was calculated using the total plant number at transplanting and the number of plants that remained after rabbits were removed from the pen.

YL assessment

According to the results of the experiment conducted in 2014 (see results for 2014), no obvious damage occurred for the heading-stage broccoli when the D_I was equated to 30 rabbits per hectare. Therefore, only seedling-stage and establishment-stage broccoli crops were assessed in 2015. Sixteen pens were prepared, and there were two replicates of each D_I (30 rabbits per hectare, 15 rabbits per hectare, 7.5 rabbits per hectare and 3.75 rabbits per hectare) at 2 crop stages (seedling and establishment) in 2015. The data from the 2014 trial was used to design the protocol for the 2015 trial and were not used in the analysis of the experimental data.

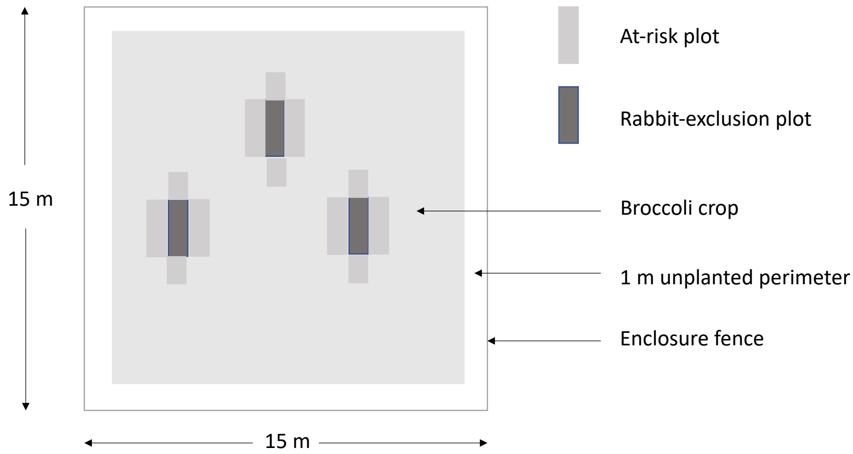

Figure 3.2 The set-up of the enclosure showing the locations of rabbit exclusion and at-risk plots in 2015, and the area planted with broccoli. Broccoli was planted 1 metre from the fence of the enclosure.

Figure 3.3 Photograph showing the experimental broccoli crop in one of the enclosures in 2015.

The first planting was from 25 May to 27 May (establishment stage), and the second planting was from 8 June to 10 June (seedling stage) to allow simultaneous comparison of two stages. Three rabbit-exclusion plots were randomly placed in each pen (Figure 3.2 and Figure 3.3). Each rabbit-exclusion plot was surrounded by 4 adjacent plots, which were treated as 2 at-risk plots. Rabbit exclusion was achieved by enclosing the plants in the rabbit-exclusion plot with a wire mesh cage (2.9 metres × 1.45 metres × 0.6 metres, mesh size 2.5 centimetres × 2.5 centimetres, 0.5 millimetres wire). A larger cage was used to prevent the plants touching the wire mesh, as occurred in the 2014 study. The cage was placed directly in the rabbit-exclusion plot one day before the introduction of rabbits. The number of broccoli plants in the rabbit-exclusion plot and at-risk plot were, respectively, 10 (n = 48 plots) and 18 (n = 48 plots) for the rabbit introduction at the seedling stage and establishment stages. The broccoli was harvested two months after being transplanted, when the heads were still green and compact. To harvest, the head was cut along with about 3–4 centimetres of stalk without any leaves. The weight of the head was recorded, and yield was expressed in tonne per hectare. YL was measured by the difference between the yield (tonne per hectare) of the rabbit-exclusion plot and the mean yield of the 2 paired at-risk plots. The mean YL of the three sets of paired plots was used as the observed YL of the pen.

It is possible that the wire mesh cages may reduce plant growth and hence the yield in the rabbit-exclusion plots. The possible effect of the wire mesh cages on the growth and yield of broccoli was tested by comparing the mean height of the broccoli plants between the exclusion plots and at-risk plots using analysis of variance (ANOVA).

3.2.4 The relationship between D_I and YL

The reduction in YL is the economic benefit of controlling rabbits (Kaboodvandpour and Leung, 2012). Equation (2) is modified to calculate the benefit/cost ratio (*R*) for the seedling stage broccoli:

$$R = V\,(YL_{un\text{-}controlled} - YL_{controlled})/C$$

$$YL_{un\text{-}controlled} = AD_I$$

$$YL_{controlled} = AD_I\,(1\text{-}E)$$

Thus

$R = VAD_IE/C$ (2)

Where V is the farm-gate value of broccoli ($tonne^{-1}$), C is the cost of control (ha^{-1}), E is the effectiveness of control expressed as the proportional reduction in rabbit density, D_I, caused by control ($0 \leq E \leq 1$). Through Equation 3, E can be defined as:

$E = RC_VA^{-1}D_I^{-1}$ (3)

D_T can be defined by setting R at 1, and the ratio of cost of control C to the value of the broccoli V as a single variable C_V, then E can be defined as:

$E = C_VA^{-1}D_T^{-1}$ (4)

3.2.5 Statistical analysis

SPSS was used to conduct simple regression for a linear relationship between YL and rabbit density (D_I), the regression was forced through the origin. Two-way ANOVA was conducted to test the effects of stage of damage and D_I on YL. For testing the possible effect of the wire mesh cage on the growth and yield of broccoli, the mean height inside and outside the rabbit-exclusion plots was analysed using one-way ANOVA (Sokal and Rohlf, 1995).

3.3 Results

2014 trial

For the seedling-stage broccoli, rabbits grazed the leaves and the stalks and pulled seedlings out of the ground, but for the establishment-stage and heading-stage broccoli, rabbits only grazed the leaves—mostly along the edge of each leaf. At the time the rabbits were removed, the average vegetative damage in the 2014 trial was substantial at 96.63% (± 0.023 SE, n = 48) for the seedling stage, 79.79% (± 0.044 SE, n = 48) for the establishment stage, and 10.96% (± 0.031 SE, n = 48) for the heading stage (Fig. 3.4). The mean damage to the plants differed significantly between the crop growth stages ($F_{2, 12} = 674.56$, $P < 0.001$), between at-risk and rabbit-exclusion plots ($F_{1, 12}$ = 3832.90, P < 0.001), and the interaction between these two ($F_{2, 12}$ = 674.56, P < 0.001).

Figure 3.4 Photos of broccoli damage caused by rabbits**.**

2015 trial

The mean height of plants before damage did not differ significantly between rabbit-exclusion and at-risk plots for the seedling stage ($F_{1, 40}$ = 0.448; P = 0.507) and establishment stage ($F_{1, 40}$ = 0.031; P = 0.862), indicating that the wire mesh cage had no effect on broccoli plant growth. Thus, it was not necessary to model the effect in the following analyses.

There were significant differences in mean YL between stage of damage ($F_{1, 40}$ = 64.346; P = 0.000), between rabbit density ($F_{3, 40}$ = 21.152; P = 0.000), and interactions ($F_{3, 40}$ = 21.951; P = 0.000).

For pens to which rabbits were introduced at seedling stage, the overall mean YL was estimated to be 1.791 tonnes per hectare (± 2.398 SE), and the mean yield of broccoli within rabbit-exclusion plots was estimated to be 4.202 tonnes per hectare (± 1.407

SE), which means 42.62% yield was lost when rabbits were released at the seedling stage. Mean YL differed significantly between D_I ($F_{3, 20}$ = 112.366, P = 0.000).

A number of potential models were fitted to the data. The linear model had the lowest AIC value (Table 3.1). At D_I = 0, no YL or yield compensation will occur, but the linear model predicted a yield compensation (1.564 tonnes per hectare). Therefore, in order to ensure biologically meaningful predictions across the range of D_I, the intercepts of the model were constrained to be zero (Figure 3.5). The form of the model was:

$YL = AD_I$ (5)

Where D_I is the density of rabbits (rabbits per hectare), YL is the yield loss caused by rabbits (tonnes per hectare), and A is the estimated rate, which was estimated to be 0.1641.

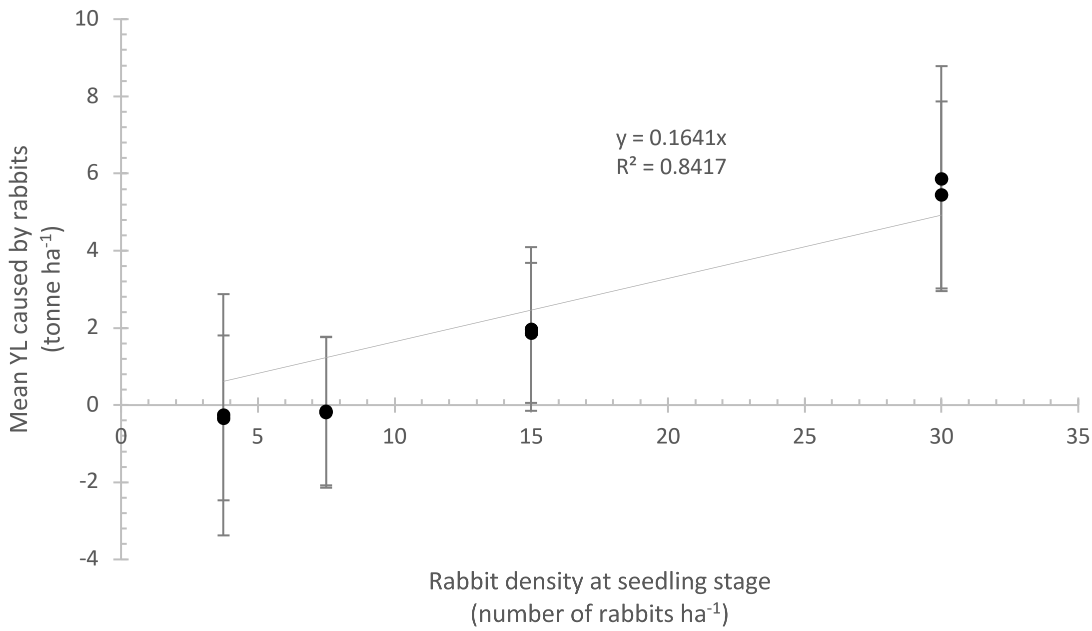

Figure 3.5 Relationship between introduced rabbit densities at the broccoli seedling stage (D_I) and yield loss caused by rabbits (YL). The linear is indicated within the data range from 3.75 rabbits per hectare to 30 rabbits per hectare. The error bar indicates the standard error.

Table 3.1 Relationships between D_I and YL caused by rabbits at the seedling stage. Akaike's information criterion (AIC) values are measures of parsimony between the fitted models and data, lower scores indicating greater parsimony.

Fitted model	Constraint	Model	R^2	Residual SS	No. of parameters	AIC
Linear	Nil	$YL = -1.564 + 0.238D_I$	0.98	0.725	n = 2	23.70
Quadratic	Nil	$YL = -1.1044 + 0.1535D_I + 0.0024D_I^2$	0.99	0.499	n = 3	32.36
Log linear	Nil	$YL = -5.0144 + 2.8764 \log(D_I)$	0.86	0.283	n = 2	36.77
Linear	Intercept = 0	$YL = 0.1641D_I$	0.84	7.344	n = 1	27.99
Quadratic	Intercept = 0	$YL = 0.0066D_I^2 – 0.0063D_I$	0.97	5.518	n = 2	38.03

For pens into where rabbits were released at the establishment stage, mean YL did not differ significantly between rabbit densities ($F_{3, 20} = 2.226$, $P = 0.117$). The overall mean YL was estimated to be 0.101 tonnes per hectare (± 0.464 SE), and the mean yield for broccoli within rabbit-exclusion plots was estimated to be 4.832 tonnes per hectare (± 1.714 SE), which means 2.09% of yield was lost when rabbits were released at the establishment stage.

3.4 Discussion

The results of the experiment demonstrated that the relationship between YL and D_I is linear when rabbit damage occurs at the seedling stage. According to Hone (2004), the linear relationship between yield of a production system and direct damage by vertebrate pests assumes no compensation. Some other studies have also reported a linear relationship between pest density and damage (Poché et al., 1982; Buckle, 2015). However, Kaboodvandpour and Leung (2012) reported that the relationship between yield loss of wheat and density of mouse was positive decelerating, and attributed this to the competition between individual mice. Given no more than 2 rabbits were present in any study pen, and alternative food (grasses) was abundant in the pen, competition between individual rabbits leading to this form of relationship was unlikely.

At the seedling stage, rabbits caused damage to whole plants, they chewed leaves, bit the stalks and even pulled up seedlings. However, when broccoli was at the establishment stage and heading stage, rabbits preferred to eat only leaves, causing no damage to the head during the entire growth stages. In addition, the damage caused by rabbits was nearly uniform for each plant; most damage occurred to leaves, especially during the establishment stage and heading stage.

For broccoli crops with rabbits present only at the establishment stage, mean YL was relatively low (0.101 tonnes per hectare, about 2.09% of overall mean yield) and was not affected by D_I. A plausible explanation for the YL was that the rabbits ate only the peripheral leaves. In addition, the low YL was possibly due to competition between rabbits (Hone, 2007) and/or overcompensation by the broccoli plants (White and Brannon, 1933). Two reasons for such competition have been presented: reduced food supply affects individual intake rate and animals interfere with each other (Hone, 2004).

For broccoli crops to which rabbits were presented at the seedling stage, D_T is calculated for the main rabbit control method commonly used by farmers in Australia. Baiting rabbits with RABBAIT® 1080 baiting (sodium fluoroacetate) was estimated to cost about \$30.69 per hectare. V was \$3,038.6 tonne^{-1} for broccoli in Queensland in 2017 (Horticulture Innovation Australian Limitied, 2018). C was therefore, 1.01% of V. Then, D_T would be 6.54 rabbits per hectare for triggering RABBAIT® 1080 carrot baiting if this method was effective in reducing D_I by 94% (Fig. 3.7). The cost of 1080 carrot baiting (in 2008) was 1.01% of the farm-gate value of broccoli, therefore, to achieve an effectiveness of > 95% control, a threshold D_I at seedling stage of 6.48 rabbits per hectare should trigger control.

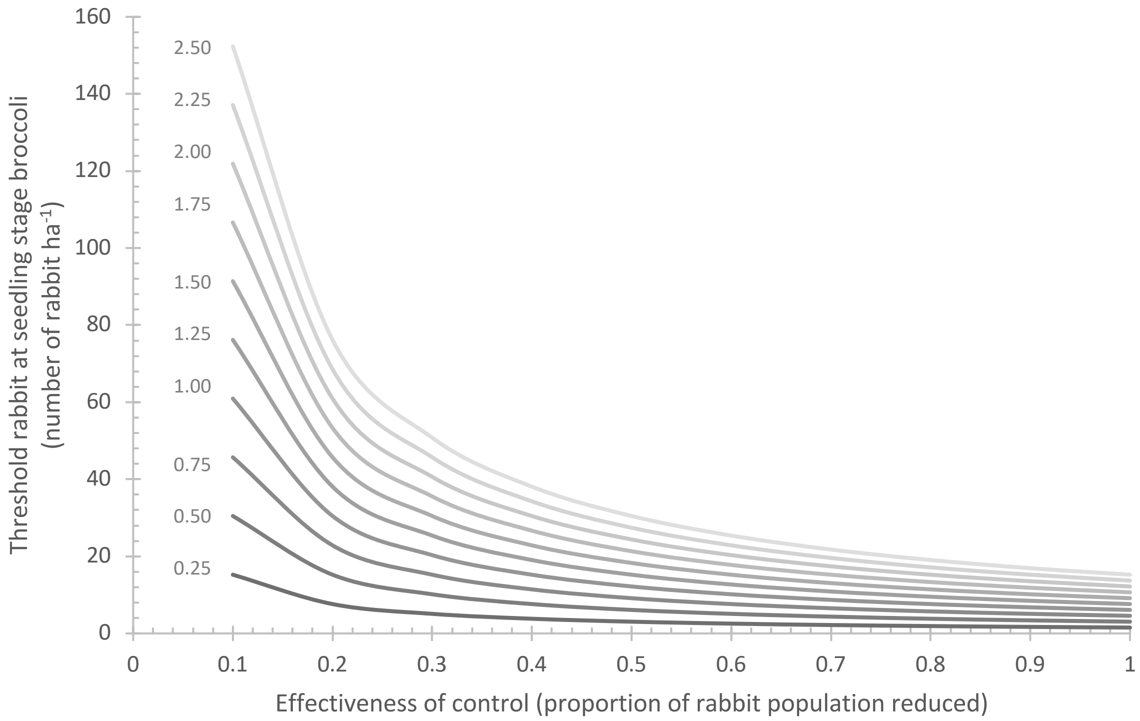

Figure 3.6 Threshold D_T for triggering control methods with varying effectiveness in reducing the introduced D_I at the seedling stage in broccoli. The curves are derived from Equation 6. The cost of control, as a percentage of the farm-gate value of broccoli (C_V) is indicated on the left of each curve. This was 20.88% for RABBAIT® Pindone Oat baiting in Australia in 2008.

In the present study there was very little biomass at the seedling stage, and rabbits removed a large proportion of the biomass well beyond the compensatory capacity of seedlings. For example, the yield of broccoli (2015–16) in the Lockyer Valley region was 7.57 tonnes per hectare (Lockyer Valley Refional Council and Stafford strategy, 2018), whereas the YL caused by rabbits in this experiment was up to 5.87 tonnes per hectare. Once the plants reached establishment and heading stages, the damage incurred was relatively low when compared to the biomass of the crop and did not lead to substantial YL. Broccoli growers would be able to use the model to calculate D_T given the effectiveness of control (E) and a specific cost structure (C_V). D_T could be reduced cost-effectively through selecting rabbit control methods to reduce C_V and increase E (Figure 3.6). D_T is the threshold to initiate control. These trials were designed to determine what level of damage could occur at different crop stages with control then being initiated to remove the rabbit pressure. This provides the lowest amount of accumulative damage to the crop. Therefore, the D_T value is a conservative one as the damage would be greater with constant pressure by rabbits over the life of the crop.

Further studies are required to determine the effectiveness of rabbit control methods (E) over a wide range of D_I in broccoli crops, because E is required to calculate D_T. Currently, E is estimated to be 89% to 98% for pindone carrot bait and 94% to 100% for 1080 carrot bait (Nelson and Hickling, 1994). However, the usefulness of these estimates was limited because D_I was not known and these were not measured in broccoli crops. The effectiveness of baiting may be low in broccoli because food supply to rabbits is usually high in this crop.

The fitted model of D_T is designed to manage YL through damage caused by rabbits at the seedling stage. The model should not be used to manage damage caused by rabbits at other growth stages. The application of the model is limited by several key assumptions that were made because of the use of pens during the experiment rather than an open field trial. First, transferring rabbits to reduce D_I was not a very viable method for a field experiment, as many factors would affect the results. Second, the cost of control and the effectiveness of the control method were assumed to be independent of D_I. However, this is unlikely to be true because with increasing D_I, more bait may be required to achieve a specific effect to reduce the rabbit population density. Third, the model assumes D_I was constant in the crop over a certain number of days. However, this may not be true in the field because the field area is much larger than the pen area; rabbit densities may vary in the field, and rabbit dispersal and density may be affected by other non-crop habitats in the field (Matthysen, 2005). Fourth, the effect of predators and biological control agents on rabbit populations is assumed to be zero in the model because predators were excluded from the pens and no biological control disease was observed in the study animals during the experiment. Fifth, the model assumes that limiting the movements of rabbits within the confines of the pen had no effect on YL. Future studies should evaluate these assumptions by quantifying these potential impacts on D_I and YL. Finally, these studies removed the rabbits after 24 days and allowed the crops to continue growing without further grazing pressure from the rabbits. This may have allowed the plants to recover from the damage without the pressure of constant damage re-occurring.

In conclusion, two strategies are recommended to reduce YL by reducing D_I in excess of D_T. First, D_I should be monitored during the seedling stage. If the D_I in the field has exceeded D_T, control should be applied. Distance sampling or a trapping web may be used to estimate D_I based on the principles of distance sampling (Lukacs et al., 2005). However, if the reduced D_I after control is still higher than D_T, substantial YL will still occur. To overcome this problem, farmers should monitor D_I well before the seedling stage so that about a week before planting D_I can be forecast by the trend in monitored densities (Kaboodvandpour and Leung, 2012). If the forecast D_I is so high that even after control the reduced density would still be higher than D_T, then additional control may be applied earlier to reduce D_I so that the final control would reduce D_I below D_T.

CHAPTER 4. The effect of simulated rabbit damage on broccoli (*Brassica oleracea* L. var. *italica* 'Anaconda') yield

Abstract

The European rabbit, *Oryctolagus cuniculus*, causes significant damage to broccoli crops in Australia by damaging seedlings, leaves and stems. I conducted this study to investigate how broccoli plants compensated for rabbit damage. I did this by manually cutting leaves to simulate rabbit damage. Potted plants were grown in a greenhouse at The University of Queensland, Gatton campus from June 2015 to January 2016. Portions of leaves from each plant were removed manually to simulate different levels of canopy damage at 0%, 5%, 10%, 25%, 50% and 80% at the seedling stage (5 leaves, 17 days after transplanting [DAT]), establishment stage (7 leaves, 28 DAT) and heading stage (11 leaves, 47 DAT). There was a significant difference in the mean weight of the broccoli head per pot at harvest (yield) for growth stage, but not for damage intensity. The mean yield adjusted for cutting intensity effect was 31.58 g ± 9.04 (SE) at the seedling stage, 38.22 g ± 4.58 (SE) at the establishment stage and 34.74 g ± 6.28 (SE) at the heading stage. At the seedling stage, there was 50% damage but little YL. Similarly, at the establishment stage, there was no significant reduction in yield as a result of damage, excepting for a significant increase in yield when the intensity of damage was 25%. The broccoli plant completely compensated for the simulated damage when the damage was imposed at the establishment and heading stages. Broccoli at earlier stages of development could not recover from damage completely as a result of inadequate ability or insufficient time to compensate. These findings have important consequences for managing the potential impacts of rabbits on broccoli crops in Australia. The results highlight that rabbit-control measures should be applied before 50% of leaves are damaged at the seedling stage.

4.1 Introduction

Vertebrate pests cause significant damage in the horticultural industry. Many studies have focused on pest management, but with little evidence of whether the damage reduced yields. Determining the relationship between damage caused and YL is central to establishing appropriate economic damage levels and economic thresholds (Carlson and Wetzstein, 1993; Wossink and Rossing, 1998; Nabirye et al., 2003; Brown, 2005). Furthermore, the full impact of a vertebrate pest on a crop is difficult to assess without knowing the potential for a plant to recover or compensate for damage (Nabirye et al., 2003; Brown and Tuan, 2005).

The European rabbit (*Oryctolagus cuniculus*) is an abundant and widely distributed introduced vertebrate pest in Australia, causing millions of dollars of losses annually for the horticultural industry. However, little is known about the economics of managing damage to a crop caused by rabbits. The rabbit is an herbivore with a diet consisting of grass, herbs and leafy weeds, and they prefer to eat foliage rather than stems, and to eat young tender plants when they are available (Millburn, 2016). It has been reported that rabbits have a preference for broccoli rather than other vegetable crops (Williams et al., 1995).

The Queensland Department of Agriculture and Fisheries (2014) reported that broccoli was one of the major cool-season vegetable crops in Queensland. In 2011, broccoli was grown in Queensland over about 1,600 hectares, producing over 10,000 tonnes of broccoli (Queensland Government Department of Agriculture and Fisheries, 2014). The area of broccoli damaged by rabbits varies between seasons and districts, with up to 100% loss in some Queensland regions, such as the Lockyer Valley (Queensland Government Department of Agriculture and Fisheries, 2014). According to the agricultural enterprises' reports which commissioned by the Queensland Department of Primary Industries and Fisheries in 2008, the estimate of the costs of rabbits to broccoli (per hectare) in Queensland was $9.05 per rabbit per year, which includes the production costs, grazing pressure and value of product (Johnson and Osmond, 2008). Rabbits can graze plants to ground level, preventing regeneration and limiting seedling establishment (Williams and Moore, 1995; Johnson and Osmond, 2008).

In the 2014 experiment (Chapter 3), rabbits damaged broccoli crops by chewing leaves along the edges and did not damage the head during the later stages of growth. Therefore, manually damaging leaves to simulate rabbit damage to young broccoli plants can provide a good measure of YL in a wide range of damage intensity at a particular growth stage. Previous studies have been conducted to simulate vertebrate pest damage to rice crops and have provided useful measures of YL at different damage intensities. For example, simulated rat damage to irrigated rice was useful for developing strategies for managing rats in Vietnam (Phung et al., 2010). Simulated house mouse damage to wheat was also useful for informing in-crop control of mice in Australia (Brown, 2005). Further examples are simulated rat damage to deep-water rice in the Philippines and Bangladesh (Guerrero, 1971; Ahmed and Haque, 1986), and to transplanted rice in Malaysia (Buckle et al., 1979). However, no studies have previously been conducted to simulate rabbit damage to broccoli.

The present study aimed to determine the relationship between simulated rabbit damage intensity and broccoli YL with single point damage (one-off) at several crop development stages. Knowledge of this relationship will be useful for developing rabbit-control plans for broccoli production.

4.2 Materials and methods

A greenhouse experiment was conducted during the spring–summer (2015-16) at UQ Gatton (27º34’S 152º20’E). The daily temperature in the greenhouse ranged from 12.3 ºC to 38 ºC, with an average daily temperature of 22 ºC. The average minimum temperature was 15.5 ºC; the average maximum temperature was 30.9 ºC, and there were 7 days when the temperature exceeded 35 ºC. Temperature was recorded using a standard thermistor probe (PB-5001), coupled to a data logger (Tinytag; Hastings data loggers, Port Macquarie, NSW, Australia).

Broccoli seedlings (two true leaves, *Brassica oleracea* L. from Withcott Seedlings) were transferred into 300-millimetre pots containing UQ Gatton standard potting mix. All seedlings were transplanted on 15 June 2015. Liquid fertiliser (Aquasol N: 23, P: 4; K: 14, S: 7 at 2.3g/L) was applied on 14 August. Plants were irrigated daily by hand as required. There were seven replicates in this experiment. The location of the pots was randomly assigned in each block (Fig. 4.1), with the pots placed 30 centimetre apart.

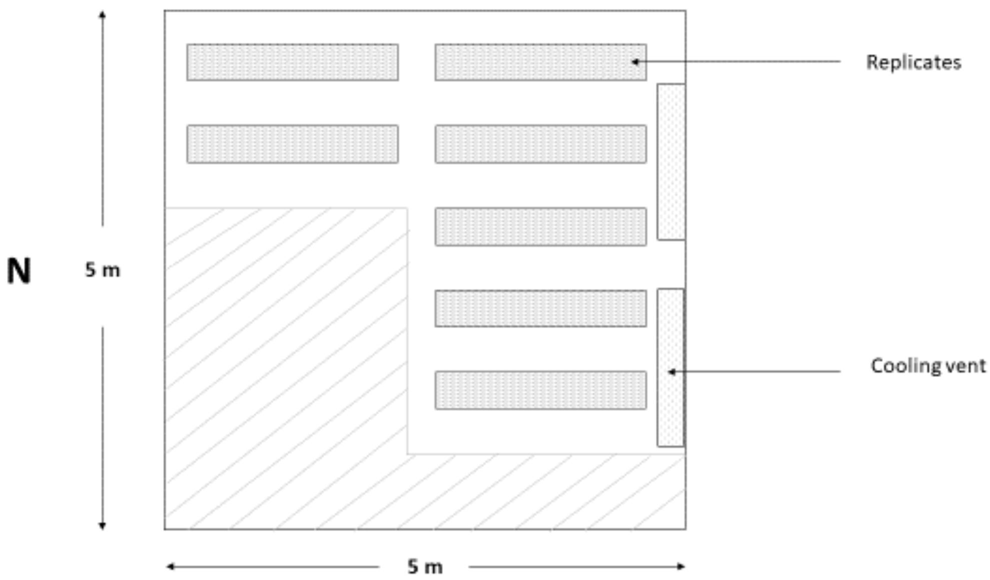

Figure 4.1 The setup of the greenhouse showing location of experimental broccoli in pots in 7 blocks.

Broccoli leaves were manually cut to simulate rabbit damage at 0% (control), 5%, 10%, 25%, 50%, and 80% of each leaf (minimum size was 5 millimetres in length) at three stages of growth: seedling, establishment, and heading. The leaf edges were cut because rabbits prefer to consume outer foliage rather than stems (Millburn, 2016). And, according to the result of the experiment in 2014 (Chapter 3), rabbit damage was observed to occur mostly on the outer leaves.

To simulate damage at different growth stages, cutting was applied on 2 July (17 DAT, seedling stage), 13 July (28 DAT, establishment stage) and 14 August (60 DAT, heading stage). Broccoli was harvested on 25 September (102 DAT, heading stage), 7 October (114 DAT, establishment stage) and 16 October (123 DAT, seedling stage). Generally, harvesting of broccoli begins about 48 days from transplant. According to some reports (Rainbowgardener, 2011), the damage caused by rabbits will delay the growth period and harvest time for a few weeks.

At completion of the experiment, the head from each broccoli plant was removed and dried at 65 ºC until, after approximately 5 days, there was no further reduction in weight. Dry weight was used to compare yield for each plant stage and damage level.

4.2.1 Statistical analyses

The IBM SPSS Statistics package was used to analyse the data. Yield data were analysed by using a two-way ANOVA procedure, using the factors of plant stage (seedling, establishment, and heading) and intensity of damage (0%, 5%, 10%, 25%, 50%, and 80%). For significant interactions, least significant difference (LSD) pairwise comparisons were conducted to examine differences between factors (Sokal and Rohlf, 1995).

4.3 Results

4.3.1 Yield

The average yield of plants with 0% damage was 31.49 grams (± 2.46 SE, n = 21) per plant. For all damage levels and plant stages, with the exception of 50% damage applied at the seedling stage, the broccoli plants overcompensated to produce a greater yield than the control plants (Figure 4.2). There was a significant difference in yield between the growth stages at which cutting occurred ($F_{(2, 108)}$ = 9.68, P = 0.001), and between levels of cut intensity ($F_{(5, 108)}$ = 2.76, P = 0.022). The interaction between cut intensity and growth stage was significant ($F_{(10, 108)}$ = 2.50, P = 0.010).

There was no significant difference in yield among different levels of damage intensity at the seedling stage ($F_{(5, 36)}$ = 2.42, P = 0.054) and heading stages ($F_{(5, 36)}$ = 1.17, P = 0.342) (Fig. 4.2). However, there was a significant difference at the establishment stage ($F_{(5, 36)}$ = 6.87; P = 0.001): a significant increase of 11.4 g pot^{-1} was recorded at the 25% cutting intensity when compared with 0% cut (42.12 g pot^{-1}, SE = 3.88 versus 31.49 g pot^{-1}, SE = 2.46, equivalent to a 33.76% increase in yield) (Figure 4.2).

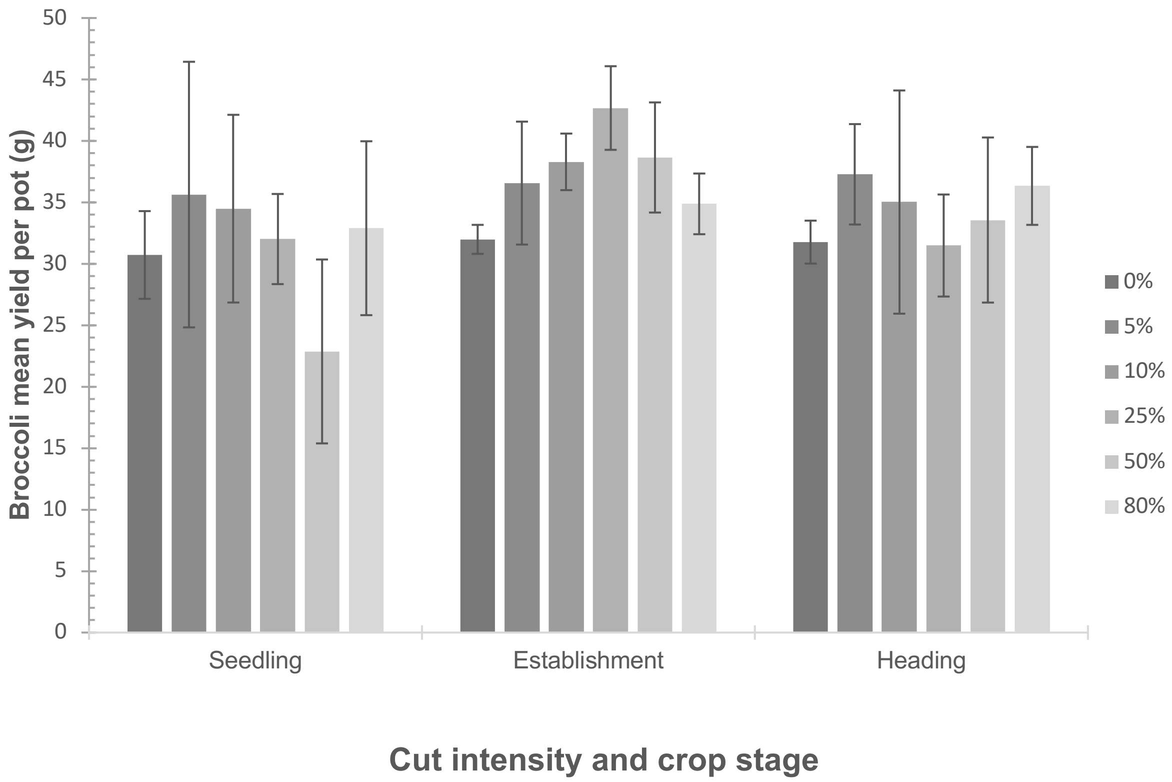

Figure 4.2 Effect of simulated rabbit damage at 0%, 5%, 10%, 25%, 50% and 80% on broccoli yield at growth stages of seedling, establishment, and heading. The error bars shown in the figure were standard errors.

4.3.2 Harvest time

From planting to harvesting of broccoli, the duration (days) of damage simulated at seedling stage, establishment stage, and heading stage was 123 days, 114 days, and 102 days, respectively.

4.4 Discussion

4.4.1 Response of broccoli plants to simulated rabbit damage

A key outcome of this experiment is that broccoli crops are able to compensate for a range of damage-intensity levels. Broccoli also compensates well for damage imposed late in the crop, at establishment stage and heading stage. These results are consistent with those of other published studies about the compensatory response of broccoli crops to damage caused by other pests (Walker, 1990; Ludwig and Kok, 1998; Ludwig and Kok, 2001; Siomos et al., 2004).

Some plants can tolerate and compensate for damage caused by herbivores (Crawley, 2009). Most compensation was through plant compensatory growth, such as damaged leaves being replaced, regrowth of roots and shoots, and increased tiller numbers (Crawley, 2009). Sherawat et al. (2007) and Phung et al. (2010), suggested a relationship between compensation and yield, although there was no consistent pattern in how the plants compensated. Broccoli plants compensated by replacing the broken leaves. The broken leaves would fall down and new leaves would grow and replace them. The total number of leaves per broccoli before harvest was similar, between 12 and 14. Also, the compensatory response of broccoli plants in my study resulted in an increase in the broccoli head weight. However, an increase in yield occurred only when the damage was simulated during the establishment stage at a low level of intensity (25%). Although damage to plants at all the other stages and intensities did not cause a statistically significant change in yield, these changes were consistently observed in one direction and suggest that damage increased yield. A similar experiment with a larger sample size would be required to provide a firmer conclusion.

Although many studies have shown that the earlier herbivory occurs and the higher the damage intensity, the lower the yield will be (Oyediran and Heinrichs, 2002). This was not reflected in the result of the present study. However, yield increases through over-compensatory growth, relative to the control, was lowest when damage was applied at the seedling stage (and negative at 50% damage), with establishment stage broccoli having a greater positive effect (yield gain) from herbivory. Levels of damage above 5% and 10% at the seedling stage resulted in lower yield increases. This may be because there was insufficient time or ability for the broccoli plant to produce as large a harvestable head by the time the plant had matured. Therefore, the timing of damage has a critical effect on the yield of broccoli crops. Similar findings have been reported for other plants, such as cabbage (*Brassica oleracea*) (Sheng et al., 2008) and wheat (Brown et al., 2010).

The harvest time of broccoli, damaged at different growth stages, differed in that the later the simulated damage was applied, the later the plants could be harvested (Figure 4.3). Crawley (2009) suggested the compensatory response by individual plants would be conditioned both by when the tissue was taken and how much was removed. When a plant is defoliated in later development stages, it may be completely unaffected by herbivory. Conversely, a plant with leaves removed at an early growth stage would need to produce new leaves to ensure sufficient carbohydrate reserves for flowering, and so crop maturation would be delayed (Rosenheim et al., 1997; Crawley, 2009). This would indicate that the time to harvest will be delayed by herbivory, particularly when damage occurs early in plant development. Broccoli produces a tightly packed central head; once removed at harvest, side-shoots with a new smaller head will appear on the stem below the cut. The broccoli will continue to produce these smaller heads for several weeks. Therefore, the harvest of broccoli will be delayed, or the yield will be reduced. A delay in harvest could prevent growers from meeting a contract order and damage their reputation as a reliable supplier of fresh broccoli. Generally, when broccoli is damaged, farmers will not wait for the plants to compensate, but pick them at the harvest, which leads to a YL. Therefore, a grower would need to control rabbits before transplanting and during the early growth stages of broccoli to avoid YL.

4.4.2 Effect on YL

When the damage happens only once during establishment stage and heading stage, broccoli could fully recover or even over compensate (Figure 4.2). This is consistent with the finding of Ludwig and Kok (2001), who conducted trials on the compensatory response of broccoli to harlequin bug *(Murgantia histrionica)* damage and reported that for broccoli, larger plants can withstand their feeding for a longer period, although they might still succumb (Ludwig and Kok, 2001). Similar results were reported by White and Brannon (1933), who showed that larger broccoli plants withstand attacks better, but the attacks can eventually lead to stunted growth. In current trial, the seedling stage showed the lowest compensatory effect (Figure 4.2). However, the relationship between YL and damage intensity was highly variable between growth stages (Figure 4.2).

Rabbits do not cause damage uniformly to individual plants, based on the results in Chapter 3. This means that the optimal time to harvest will differ between individual plants because each plant has a different level of damage caused by rabbits. Given harvesting takes place once, growers will have to make a decision on the timing of harvest to minimise YL caused by plants being not ripe enough or overripe for harvest.

Nevertheless, the results of this experiment are still useful in helping growers make an informed decision by predicting the timing of harvest, based on the negative linear relationship between timing of damage and time to harvest.

Simulating rabbit damage to broccoli in a greenhouse is not the same as natural damage caused by rabbits under field conditions, because the distribution of the pest throughout the crop affects the level of damage (Phung et al., 2010). However, in this experiment, only leaves were cut to simulate rabbit damage, as cutting the stems generally caused plant death. Also, in a greenhouse, there were few adverse effects of environmental conditions on broccoli growth, such as strong winds or other pests, and there were some positive effects, such as managed nutrition and water availability. Therefore, the results from my research could be considered as a maximum yield response. The results from this experiment can be applied only to plants which are grown under similar conditions, have similar duration of growth and to which similar agricultural practices have been applied. They do provide an indication of the ability of broccoli to compensate for damage such as might be caused by rabbits in the field.

In conclusion, broccoli plants are able to totally compensate for simulated rabbit damage at the establishment stage and heading stage. However, broccoli plants would not be able to compensate for simulated damage intensity of 50% at the seedling stage. These findings have important consequences for managing potential impacts of rabbits on broccoli crops in Queensland in terms of the timing of rabbit control and damage assessment. The results confirm that the damage and YL were highly variable and that compensation occurred from the seedling stage to heading stage. Also, the data indicated the timing of damage had a significant effect on broccoli yield, and the seedling stage is the key time for growers to control rabbits.

CHAPTER 5. A field trial to assess the effects of rabbit grazing on corn

Abstract

Maize is ranked 5th in terms of crop production in Queensland, and is used for stockfeed and industrial uses. However, there is little information on the effects of rabbit (*Oryctolagus cuniculus)* grazing on this crop. The aim of this study was to assess the effects of rabbit grazing on corn. This study was conducted at a rabbit and predator-proof enclosure at UQ Gatton campus over the summer cropping season in 2016. Corn was grown in 15 enclosures following current agronomic procedures, and was subjected to grazing by 2 densities of rabbits (44.44 rabbits per hectare and 88.89 rabbits per hectare) at three different growth stages: emergence (7 days after sowing [DAS]), tillering (21 DAS) and tassel (42 DAS). Rabbit grazing resulted in a significant decrease in the survival rate and yield of corn plants at the emergence stage, and with some plants producing immature cobs or no cobs at all, and a delay in plant growth and harvest. In addition, the number of corn ears per pen was significantly reduced by rabbit grazing, which is crucial in estimating corn yields. The emergence stage is the critical stage to control rabbits as rabbit grazing resulted in large losses in corn production during the early growth season. This new information provides farmers with a better understanding of the damage caused by rabbits, enabling them to make more informed decisions as to whether their crop needs to be protected from rabbits, when rabbits should be managed, and how to manage rabbits.

5.1 Introduction

The introduced European rabbit is one of the most important pests in Australia (Williams et al., 1995). It causes damage to crops, pastures and native vegetation, causing severe economic and environmental impacts (Myers et al., 1994; Lees and Bell, 2008). Rabbits have spread in the Lockyer Valley, an important vegetable growing region in Australia (Gould, 2014). Compared with some other summer crops, such as cotton and sorghum, corn is a relatively minor crop both in production and area (Grains Research and Development Corporation, 2017). However, in the Lockyer Valley, corn is an important crop. Corn is ranked 5th in terms of production in Queensland, after wheat, sorghum, cottonseed and barley (Grains Research and Development Corporation, 2017). In 2017, Australia's corn acreage was 64,000 hectares, with an annual production of 440,000 tonnes, or 6.875 tonnes per hectare (AgriFutures Australia, 2017). The production of corn is used by a wide range of industries, varying from stockfeed, starch extraction, and snack foods to breakfast cereals. Corn is also grown for silage (Extension, 2008).

Rabbits are economically the most important agricultural pest in Australia, causing more than $200 million in pre-harvest production losses each year (Cooke et al., 2013). However, there are few published reports on damage to corn caused by rabbits. According to Mason (2016), corn is one of the crops which suffers little damage from rabbits. Reports from corn growers in the Lockyer Valley, however, indicate rabbits caused severe damage to corn and that they prefer to sow again after this severe damage. Gough (1955) reported corn fields (*Zea mays*) were severely grazed by rabbits in England. The author suggested that such damage caused a delay in plant establishment and retarded the formation of secondary roots and tillers. Gough and Dunnett (1950) also suggested that for some crops, the earlier the damage occurred, the more severe the damage. However, the degree of rabbit grazing damage to cereal crops is difficult to estimate quantitatively throughout the growing season (Thompson and Worden, 1956). Crawley (1989) monitored different densities of rabbits and their damage to winter wheat and reported the effect of timing of rabbit damage on yield. Bell et al. (1998) used enclosed rabbits to determine the effect of rabbit damage on the growth and yield of winter cereal in Ireland.

Currently, there is paucity of information about damage to corn caused by rabbits. Therefore, I carried out this study to investigate the effects of rabbit grazing on corn production. Mckillop et al. (1996) developed a model to assess the effects of rabbit grazing on a field site in Hampshire. Dendy et al. (2004) used this model to predict the YL of winter wheat caused by rabbit grazing on spring barley. This knowledge may be useful in developing strategies to manage rabbits in corn crops.

5.2 Materials and methods

5.2.1 Experimental approach and study site

To assess the effects of rabbit grazing on corn, two different densities of rabbits (44.44 rabbits per hectare and 88.89 rabbits per hectare) were introduced and kept for 7 days in corn crops at three growth stages (emergence, tillering and tassel). The crop was enclosed by rabbit-proof fences, and the plant survival rate and yield (tonnes per hectare) were measured.

The corn was feed/silage corn (Pacific Seeds Company, pac 607IT). The stress tolerance of this corn was 7, with the rating scale ranging from 1 to 9. The stress tolerance means the ability of plants to be resistant to disease, or more tolerant to an abiotic stress (in some cases, to more than one abiotic stress) (Rai and Takabe, 2006). The abiotic stress can include drought, cold, heat, and hyperosmotic stress, salt or low nitrogen conditions (Rai and Takabe, 2006). The rating of 7 indicates the ability of plants to tolerate most stresses during the growing period, such as cold, heat, moisture, etc. Thus, in most cases, pac 607IT would not be affected by weather.

This experiment was conducted in rabbit proof pens at the UQ Gatton campus wildlife enclosures (27º34'S 152º20'E) from November 2015 to April 2016. The average monthly temperature ranged from 12.6 °C to 39.8 °C, average monthly rainfall was 59.97 millimetres, and the evaporation rate was 681.0 millimetres (Australia Bureau of Meteorology, 2016). The soil at the study site is a self-mulching, cracking alluvial soil, which is similar to, but sandier than the black soil typically used for field crops in the Lockyer Valley. To emulate the habitat condition of field crops (e.g. alternative food and water supply to rabbits), and to reduce possible effects of other environmental conditions, the corn was grown under typical field crop conditions using standard agronomic practices, such as land preparation, planting density and irrigation. The crop field was irrigated by a local crop farmer according to everyday weather conditions.

5.2.2 Experimental animals

Ten rabbits were trapped from farms around UQ Gatton and housed in a pen (15 metres × 15 metres) for acclimatisation and disease monitoring for one month. Four shelters were prepared for rabbits in the pen. Mixed vegetables, local plants and clean water were provided during acclimatisation. Rabbits were adults, with body weights ranging from 1200 to 2000 grams. Only female rabbits were used in this experiment. Rabbits were assigned to the experimental pens to ensure their body weight and conditions were similar across pens. Experimental rabbits were marked by ear tags (Ohrmarken, model 73850, made by Hauptner, Zurich) for individual identification. This study was conducted under the University of Queensland Animal Ethics Approval numbers: SAFS/152/15/DAFF and DAFF/SAFS/200/14.

5.2.3 Introduced D_I

Three rabbit population densities were introduced at the emergence stage (7 days after sowing; DAS), tillering stage (21 DAS) and tassel stage (42 DAS) by releasing 0, 1 and 2 rabbits in each pen and keeping them there for 7 days over a 2-week period: 0; 44.44; and 88.89 rabbits per hectare, respectively. The maximum population density used in the introduction was lower than the maximum estimated population density of rabbits in the field in Australia (280 rabbits per hectare) (Berman et al., 1998). There were 7 different experimental groups: 2 pens with no rabbits (0 rabbits per hectare; control group); pens with 1 rabbit released (44.44 rabbits per hectare) at the emergence stage (2 pens), tillering stage (2 pens) and tassel stage (2 pens); pens with 2 rabbits released (88.89 rabbits per hectre) at the emergence stage (2 pens), tillering stage (2 pens) and tassel stage (2 pens). The control group was not independent between the growth stages because the 2 same pens were used over the 3 growth stages, and this is justified because no rabbits were released into the pen and there were not enough pens for full replication.

In addition, there was a pen with 2 rabbits introduced and kept for all the growth stages and one pen was used for housing rabbits Thus, a total of 16 pens (15 metres × 15 metres) were used in this study (Figure 5.1).

Figure 5.1 The experimental groups were randomly allocated to 15 rabbit-proof pens. An additional pen was used for housing rabbits.

5.2.4 Data assessment

On 2 December 2015, 36 seeds were sown per bed into 12 pre-prepared beds in all pens, with each seed 30 centimetres apart. The resulting density of planting was 19,200 plants per hectare (density rates for corn in Queensland range from 15,000 to 70,000 plants per hectare with most from 50,000 to 60,000 per hectare; Wright et al. 2005). Each bed was 13 metres x 0.80 metres. Corn was harvested for yield assessment on 22 February (83 DAS). To reduce edge effects, 3 plants at both ends of each row and the first and last row of each pen were not used for data collection. Rabbits were released at the emergence stage (7 DAS), tillering stage (21 DAS) and tassel stage (42 DAS).

To investigate the effects of rabbits grazing on corn, the survival rate of plants and the percentage of corn producing 1 ear or more than 2 ears were counted and calculated. The number of plants producing 1 ear or 2 ears counted at harvest was compared with the number of plants remaining after rabbits were introduced at the emergence, tillering and tassel stage.

To estimate corn yield, 20 plants in each pen were randomly selected and marked before rabbit release. The size and number of kernels per ear and the number of ears per plant were estimated and counted, kernels near the tip and butt which were less than half the size of kernels midway up the ear were not counted.

According to Lee and Herbek (2005), ultimate corn yield depends on number of ears per acre, number of kernels per ear, and average weight per kernel. Equation to estimate corn yield:

$$Ultimate\ corn\ yield\ (bushels/acre) = \frac{(kernels\ per\ ear) \times (ears\ per\ acre)}{kernels\ per\ bushel}$$

$$1\ bushel\ per\ acre = 0.06725\ tonnes\ per\ hectare$$

The simplest and least accurate method is to count the number of kernels per ear and multiply by 0.300 to get a very rough yield estimate (Lee and Herbek, 2005). However, the kernel size (kernels per bushel) is affected by stressful weather conditions and growing conditions (Lee and Herbek, 2005). To adjust for differences in kernel size, the multiplier was 0.191 for small kernels, 0.233 for medium kernels, and 0.300 for large kernels (Lee and Herbek, 2005).

5.2.5 Statistical analysis

IBM SPSS Statistics was used to conduct a two-way ANOVA, fixing the following factors: growth stage of corn when damage occurred (emergence, tillering and tassel), and densities of rabbits per hectare (0, 44.44 and 88.89). Least significant difference (LSD) pairwise comparisons were conducted to determine significant differences (Sokal and Rohlf, 1995).

5.3 Results

There were significant differences in mean survival rate of plants between rabbit densities ($F_{2,\ 7}$ = 725.164, P < 0.001), between growth stages of damage ($F_{2,\ 7}$ =

1804.164, P = 0.000), and interaction between D_l and growth stage was significant ($F_{2, 7}$ = 734.715, P = 0.000). The mean survival rate for plants with 1 rabbit released at the emergence stage was significantly lower than that at the tillering stage and tassel stage ($F_{2, 3}$ = 1563.431, P = 0.000). For pens with 2 rabbits released, the mean survival rate for plants with damage occurring at the emergence stage was significantly lower than those with damage occurring at the tillering stage and tassel stage ($F_{2, 3}$ = 1075.308, P = 0.000).

When 2 rabbits were released at the emergence stage, all plants were destroyed. When 1 rabbit was released at the emergence stage, more than 20% of plants were destroyed. Less than 5% of plants were destroyed when 1 rabbit was released at the tillering and tassel stages. The number of plants remaining in the pen to which rabbits were introduced at the emergence stage was much lower than that in which rabbits were introduced at other stages. In addition, for the pen in which 2 rabbits were kept continuously, all seedlings were destroyed by the rabbits within the first few days.

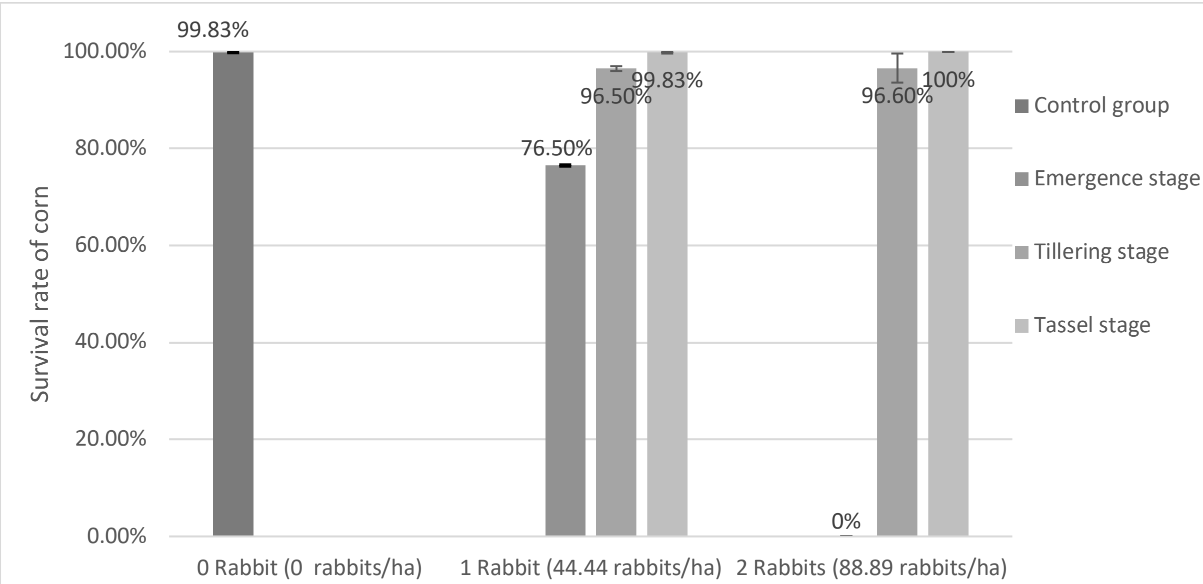

Figure 5.2 Mean survival rate of corn plant after rabbits at 2 densities per hectare (0, 44.44 and 88.89) were introduced and kept for 7 days at emergence, tillering and tassel stages. Shown are means ± SE for each density of rabbits and crop stage when damage occurred.

Table 5.1 Rabbit grazing damage to corn in 2015. After rabbits had been released into each pen for 7 days, the ratio of plants producing mature, immature, and no cobs for each experimental group were counted. Also, the ratio of plants producing 1 mature cob and more than 1 mature cobs were counted.

	Control (0 rabbit)	1 rabbit (44.44 rabbits ha^{-1})			2 rabbits (88.89 rabbits ha^{-1})		
		Emergence Stage (7 DAS)	Tillering Stage (21 DAS)	Tassel Stage (42 DAS)	Emergence Stage (7 DAS)	Tillering Stage (21 DAS)	Tassel Stage (42 DAS)
Plant produce mature cobs (%)	99.83%	18.67%	86.33%	99.83%	0%	73.17%	100%
Plant produce immature cobs (%)	0%	18.83%	3%	0%	0%	8.3%	0%
Plant produce no cobs (%)	0%	39%	7.17%	0%	0%	15.17%	0%
Plant produce 1 mature cob (%)	99.83%	6.83%	65.33%	99.83%	0%	46.83%	100%
Plant produce more than 1 mature cobs (%)	0%	11.84%	21%	0%	0%	26.34%	0%

The ratios of plants producing mature cobs for pens in which rabbit grazing occurred at the emergence stage were much lower than other stages. The ratio of plants producing more than 1 cob for pens where rabbit grazing occurred at the emergence stage and tillering stage was much higher than at the tassel stage and for control groups. For pens in which only 1 rabbit was released at the emergence stage, over 18% of plants produced immature cobs and 39% of plants produced no cobs, while only 18.67% of plants produced mature cobs, and less than 7% produced 1 cob (Table 5.1).

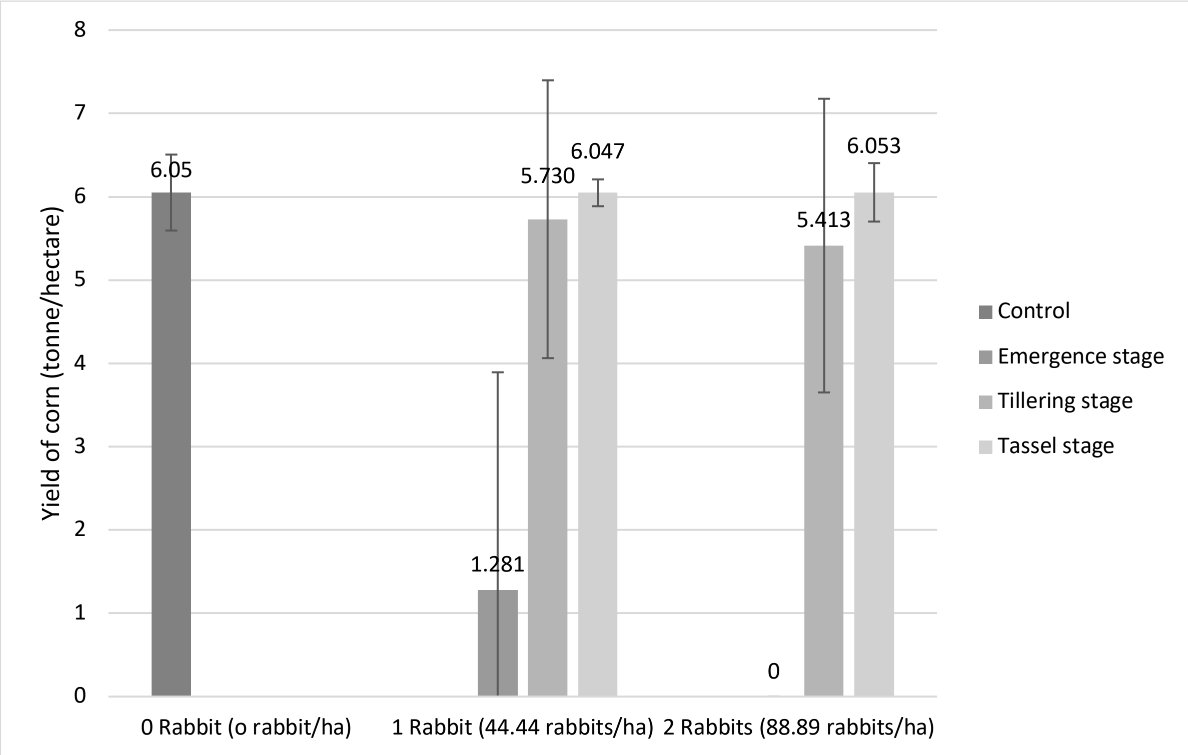

Figure 5.3 Effect of rabbit grazing on corn: yield of corn (tonne per hectare). Shown are means ± SE for each density of rabbits and crop stage when damage occurred.

The mean yield for control groups was 6.05 tonnes per hectare (± 0.46 SE, n = 40). There was a significant difference in yield between stages of damage ($F_{2, 273}$ = 374.802; P = 0.000), between rabbit densities ($F_{1, 273}$ = 8.831; P = 0.003), and interaction between rabbit density and stage of damage was significant ($F_{2, 273}$ = 4.678; P = 0.010) (Figure 5.3).

The mean yield for plants to which damage occurred at the emergence stage was significantly lower than for those damage occurred at the tillering stage, tassel stage and for the control groups (0.64 tonnes per hectare ±1.95 SE versus 5.57 tonne per hectare ± 1.72 SE, 6.06 tonnes per hectare ± 0.26 SE and 6.05 tonnes per hectare ± 0.46 SE, equivalent to 88.51%, 89.44% and 89.42% reduction in yield, P = 0.003) (Figure 5.3). At the emergence stage, there were significant reductions in yield for plants where 1 rabbit was released compared with damage that occurred when 2 rabbits were released (1.281 tonnes per hectare ± 2.61 SE and 0 tonnes per hectare ± 0 SE, respectively; P = 0.003).

5.4 Discussion

Plant growth was affected by rabbit grazing, with a significant decrease in the survival rate of plants and yield when grazing occurred at the beginning of the cropping period (emergence stage). Although there appeared to be little difference in the number of plants surviving grazing when rabbit grazing occurred at the tillering stage, more plants produced immature cobs or no cobs at all compared with the control-groups plants. These findings suggest that plants are unable to recover from the damage caused by early grazing and its effects are still clearly shown at harvest. In addition, the ratio of plants producing mature, immature, or no cobs indicated that plant growth was delayed by rabbit grazing (Table 5.1).

Once the corn plant reached 1.27 metres in height, it was difficult for rabbits to cause damage because they did not chew the stem when other food was available. Cobs are produced in the upper parts of the plant and are well out of reach of rabbits. In addition, rabbits prefer to chew leaves of early stage corn rather than leaves and stalks of mature corn plants. Therefore, when damage occurs at the emergence stage and tillering stage, the damage will affect the entire plant, including the yield. However, when damage occurs at the tassel stage, plants will lose lower leaves due to grazing by rabbits, but this does not greatly affect cob production. Similar results have been reported by Gough and Dunnett (1950), who indicated the earlier the damage occurred, the more severe the damage; and rabbit damage would delay plant establishment and destroy plants by retarding or preventing the formation of secondary roots and tillers.

Plant population is not a reliable indicator of yield because some plants may not produce ears and others may have two or more ears in compensation. According to Lee and Herbek (2005), ultimate corn yield depends on the number of ears per acre, number of kernels per ear and average weight per kernel. The number of kernels per ear is crucial in estimating corn yield (Lee and Herbek, 2005). Results showing the ratio of plants producing mature ears per plant appeared to indicate that rabbits' grazing resulted in a significant reduction in the number of mature ears of corn. However, plants damaged by rabbits during the early growth stage will compensate. This compensation will result in a significant increase in the number of cobs per plant.

Therefore, some plants which were damaged at the early growth stage produced more ears than undamaged ones, if there was enough time for regenerated tillers to sufficiently mature (Lv et al., 2008). However, even if given enough time, this plant compensation cannot compensate for the loss of overall production, especially when rabbit damage occurs at the emergence stage.

The experiment is limited by several key assumptions that were made because of the use of pens during the experiment rather than having an open field trial. The effect of rabbit grazing may be different in field than in enclosed area, because the pen was very small and may affect the dispersal and density of rabbits; rabbit densities may vary within a crop planted in a large area. In addition, vines (weeds) grow rapidly in some pens in the fifth week after sowing. The stress tolerance of the corn is high, which means the corn might be able to tolerate the stress from vines, but there was no evidence that vines had no effect on the growth of corn.

Conducting research to determine and predict the level and costs of damage is extremely important for farmers because it enables them to determine the cost-effectiveness of different control strategies and to make more efficient use of their land (Dendy et al., 2004). Planting is the single most important operation in the farming system (Grains Research and Development Corporation, 2017). Corn, as well as other crops, such as soybean, does not have the ability to completely compensate and recover from damage during the emergence stage (Corn yield potential, 2008). Therefore, it is important to ensure that emerging seedlings are protected from seedling pests (Grains Research and Development Corporation, 2017). Establishing a uniform, optimum population stand is the first step in developing corn-grain yield potential (Corn yield potential, 2008).

First, farmers should monitor their crops as frequently as once a week as suggested by the Queensland Government sweet corn information kit (Wright et al., 2005). Second, if plants have been chewed off by rabbits, an electric fence or netting should be built around the perimeter of the block. A diagram of an electric fence designed to keep rabbits and hares out of crops has been designed and displayed by the Queensland Government (Fig. 5.3).

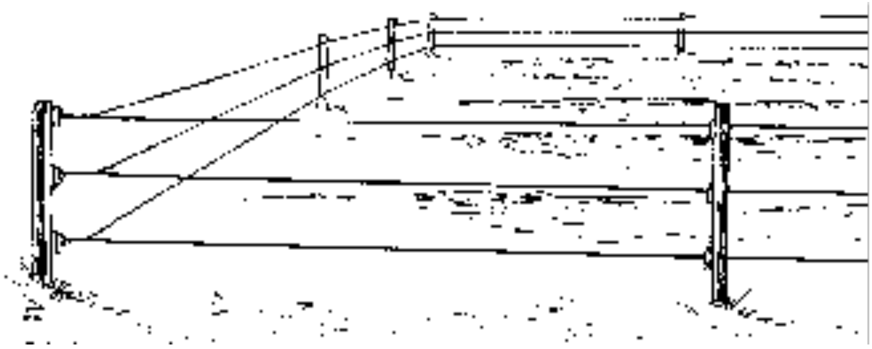

Figure 5.4 A diagram of an electric fence to exclude rabbits and hares from crops (Wright et al., 2005).

CHAPTER 6. General discussion

In my thesis, a series of manipulative experiments was used to determine density thresholds to manage rabbit damage to broccoli and corn. This final chapter provides a brief summary and synopsis of the research work, including a short discussion of results emerging from the integration of the preceding chapters. This final chapter is framed around the key questions posed in Chapter 1, and draws on the findings of the three research chapters.

6.1 What is the difference between rabbit damage and mouse damage?

The house mouse (*Mus domesticus*) is a small mammal of the order Rodentia, which is one of the most important model organisms in biology and medicine. The rabbit (*Oryctolagus cuniculus*) belongs to the Lagomorph family. They are different orders. However, in the area of pest control, there are similarities between rabbits and mice, such as they are both widespread, and they could cause serious damage to agricultural and horticultural industries during the early growth stages of grains. The house mouse is a typical pest control model in Australia. Therefore, large numbers of articles related to mice were cited in Chapter 1 to 4. In addition, research designs similar to those used for studying house mouse damage—such as modelling density thresholds and simulating damage to crops—were used in Chapter 3 and 4. However, the difference between them cannot be ignored. The house mouse can dig up and eat newly planted seeds, cut stems, and eat developing grain (Brown, 2005). However, significant damage always occurs at the later stages of crop growth, particularly after mice begin their breeding season in early spring (Brown and Singleton, 2001). In addition, unlike rabbits, mice eat broccoli heads and cobs of corn. Rabbits are grazers and prefer to eat the green leaves rather than broccoli heads and cobs of corn. Therefore, the damage caused by rabbits to crops always occurs during the early growth stage.

For these reasons, when designing the experiments, I introduced certain densities of rabbits to broccoli crops at different growth stages (Chapter 3), I simulated rabbit damage to broccoli (Chapter 4), and used similar experimental models for house mice and rabbits. Because of the difference between rabbits and house mice, however, there were many differences between the house mouse experiments and the rabbit experiment, such as cutting leaves of broccoli (rabbit) instead of cutting tillers of wheat (house mouse) (Chapter 4).

6.2 What is the relationship between D_I and broccoli YL?

In Chapter 3, a relationship between damage (YL) to broccoli and D_I was established through introducing known D_I at the seedling, establishment, and heading stages of broccoli crops. Three patterns of the relationship between D_I and YL were categorised:

1. When rabbits were introduced at the seeding stage, the relationship between D_I and YL was linear, with YL increasing as D_I increased. D_T would be 6.54 rabbits per hectare for triggering RABBAIT® 1080Carrot Bait if this method was effective in reducing D_1 by 94%.
2. When rabbits were introduced at the establishment stage, there was no significant relationship between D_I and YL.

The linear relationship between D_I and YL at seedling stage is best explained as follows. Young plants were most sensitive to damage with increasing YL with increasing D_I early in the crop growth (around seedling stage and establishment stage).

Similar results showing a linear relationship between pest density and damage have been found in other pests (Poché et al., 1982; Buckle, 2015).

6.3 How do broccoli plants compensate for damage caused by rabbits?

In Chapter 4, I examined the response of broccoli crops to simulated rabbit damage. The plants compensated well for damage imposed later in development—at the establishment stage and heading stages. Similar results have been reported for other pests in broccoli crops (Walker, 1990; Ludwig and Kok, 2001; Phung et al., 2010).

All levels of damage across all stages of crop growth were simulated, and the resulting compensatory responses provide a good understanding of how broccoli plants compensate for single-point (one-off) damage. This approach could be used for a range of other vertebrate pests (e.g. mice, kangaroo and duck).

6.4 What are the effects of rabbit grazing on corn?

In Chapter 5, I reported on the effects of rabbit grazing on corn. This was assessed by releasing 2 densities of rabbits (44.44 rabbits ha^{-1} and 88.89 rabbits ha^{-1}) in the emergence, tillering and tassel stages of corn crops. Three effects of rabbit grazing were found:

1. Rabbit grazing results in a significant decrease in the numbers of plants, and in the yield of corn at the emergence stage.
2. Rabbit grazing delayed the growth and maturity of corn.
3. Corn would compensate for rabbit grazing through increasing the number of mature ears per plant.

To resist or reduce the effects of rabbit grazing, corn growers should frequently monitor their crop—at least once per week up to the tassel stage, then twice a week up to harvest. In addition, an electric fence or a netting enclosure should be built around the perimeter of the block to resist rabbits.

6.5 General discussion

The results of these experiments indicate that the rabbit has a strong ability to destroy broccoli and corn crops. However, broccoli would be able to compensate for this when damage occurred at early growth stages (Chapter 4).

6.5.1 Management implications

The findings highlight the need to conduct rabbit control in the field to limit damage before the threshold is exceeded. Ideally, rabbits should be controlled before plants are transplanted or during the emergence stage.

Farmers generally conducted rabbit control after there had been high crop losses. In Chapter 3, the effect of reducing D_l on YL was modelled using data for the RABBAIT® Pindone Oat Bait. The modelling suggested that there was about a 94% reduction in density required to minimise YL for seedling-stage broccoli.

Growers need to estimate rabbit densities, especially before sowing or transplanting broccoli seedlings, to know if it is economical to apply bait. Some methods have been provided to index and monitor rabbit numbers in the field, such as spotlight and headlight counts, footprint counts, and warren counts. However, spotlighting is not a reliable index when rabbit numbers are low. For a good estimate of numbers in a small area, footprint counts and camera traps are more precise, alternative methods for indexing rabbit numbers (Caley and Morley, 2017). In addition, the pellet count method that Mutze et al. (2014) developed could be useful. Essentially, the farmer only needs to know if rabbits are present or not. Active warren-opening counts will not provide an accurate index of rabbit numbers because in the Lockyer Valley most of the rabbits are living above ground or in log piles (Rusli, 2015).

There are many methods available for farmers to reduce the damage caused by rabbits, including shooting, biological control, warren ripping, and baiting. Rabbit control is best done by the growers after monitoring rabbits in the field. Farmers should work together as a community to control rabbits on a large scale using a combination of control methods with the following strategies:

1. Control management should be focussed at all times because rabbits breed throughout the year.
2. Destroy warrens and shoot rabbits before sowing or transplanting crops; monitor and hunt rabbits during the early stage of growth.

6.5.2 Future directions

The findings from my thesis highlight the fact that additional research is required to develop more precise density/damage relationships for rabbits in corn and broccoli crops using larger sample sizes. This study has provided data on the threshold population density of rabbits and the key time for rabbit control. However, how do rabbit populations recover from control? What is the speed of the recovery, and what would affect the recovery? Answers to these research questions will further advance this area of pest management science.

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Appendices

Appendix 1: Broccoli planting in 2014, and 4 rabbit-exclusion plots were set in each pen.

Appendix 2: European rabbit (*Oryctolagus cuniculus*) chewing vegetable on 20 August 2014. Rabbits prefer leaves rather than broccoli head.

Appendix 3: Broccoli harvest in 2014 (chapter 3), broccoli was damaged by rabbits (30 rabbits/ha) at seedling stage.

Appendix 4: Broccoli harvest in 2014 (chapter 3), broccoli was damaged by rabbits (30 rabbits/ha) at establishment stage.

Appendix 5: Broccoli harvest in 2014 (chapter 3), broccoli was damaged by rabbits (30 rabbits/ha) at heading stage.

Appendix 6: The arrangement of broccoli in greenhouse, damage density of each plant was marked on the white tag.

Appendix 7: The vines caused severe stress to corn

Appendix 8: Tassel stage corn harvest without any damage, and each plant growth only one mature ear with brown silk.

Appendix 9: mature cob with brown silk

Appendix 10: The copy of Animal Ethics Approval Certificates

THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

UQ Research and Innovation
Director, Research Management Office
Nicole Thompson

Animal Ethics Approval Certificate

09-Jun-2015

Please check all details below and inform the Animal Welfare Unit within 10 working days if anything is incorrect.

Activity Details

Chief Investigator:	Peter Elsworth
Title:	Impact of rabbit density/activity on vegetable production
AEC Approval Number:	SAFS/152/15/DAFF
Previous AEC Number:	
Approval Duration:	09-Jun-2015 to 09-Jun-2018
Funding Body:	DAFF
Group:	Production and Companion Animal
Other Staff/Students:	Ruishu Wang, Mark Rusli, Patrick Webster, Michael Brennan, Luke Leung
Location(s):	Gatton - Wildlife Unit

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Rabbits		Adults	Mix	Natural Habitat	45	45

Permits

Declared Pest Permit 0595-01-SRC-003 01-Jul-2014 to 17-Apr-2016

Provisos

Pest Species (Rabbits) Proviso:
Rabbits are a pest species held at UQ by a DAFF permit and as such all permit conditions must be adhered to including the following:
a) Rabbits must be preferably micro chipped (or some other permanent marking used) for identification purposes and be housed according to the DAFF permit regulations
b) The CI must ensure that the rabbits are well identified and accurate records are kept of their use.

Approval Details

Description	Amount	Balance
Rabbits (Mix, Adults, Natural Habitat)		
9 Jun 2015 Initial approval	45	45

Animal Welfare Unit
UQ Research and Innovation
The University of Queensland

Cumbrae-Stewart Building
Research Road
Brisbane Qld 4072 Australia

+61 7 336 52925 (Enquiries)
+61 7 334 68710 (Enquiries)
+61 7 336 52713 (Coordinator)

animalwelfare@research.uq.edu.au
uq.edu.au/research

UQ Research and Innovation
Director, Research Management Office
Nicole Thompson

Animal Ethics Approval Certificate

28-Oct-2014

Please check all details below and inform the Animal Welfare Unit within 10 working days if anything is incorrect.

Activity Details

Chief Investigator:	Dr Luke Leung, Agriculture and Food Sciences
Title:	Pen studies to assess rabbit damage to horticultural crops (CA2014/04/758)
AEC Approval Number:	DAFF/SAFS/200/14
Previous AEC Number:	
Approval Duration:	26-Jun-2014 to 26-Jun-2017
Funding Body:	
Group:	Production and Companion Animal
Other Staff/Students:	Peter Elsworth, Ruishu Wang
Location(s):	Gatton - Wildlife Unit

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Feral Rabbits		Adults	Mix	Other	0	0

Permits

Provisos

Animal numbers are not shown on this approval certificate, as the approved animal numbers are provided under DAFF CA2014/04/758 AEC Approval.
This certificate is to show that the project has been ratified by a University of Queensland AEC.

Approval Details

Description	Amount	Balance
Feral Rabbits (Mix, Adults, Other)		
18 Jun 2014 Ratification	0	0

Animal Welfare Unit
UQ Research and Innovation
The University of Queensland

Cumbrae-Stewart Building
Research Road
Brisbane Qld 4072 Australia

+61 7 336 52925 (Enquiries)
+61 7 334 68710 (Enquiries)
+61 7 336 52713 (Coordinator)

animalwelfare@research.uq.edu.au
uq.edu.au/research

THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

UQ Research and Innovation
Director, Research Management Office
Nicole Thompson

Animal Ethics Approval Certificate

26-Nov-2014

Please check all details below and inform the Animal Welfare Unit within 10 working days if anything is incorrect.

Activity Details

Chief Investigator:	Peter Elsworth
Title:	Rabbit surveys and crop damage assessment
AEC Approval Number:	DAFF/431/14
Previous AEC Number:	
Approval Duration:	19-Nov-2014 to 19-Nov-2017
Funding Body:	
Group:	Production and Companion Animal
Other Staff/Students:	Luke Leung, Patrick Webster, Mark Rusli, Riushu Wang
Location(s):	Other Queensland Location

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Rabbits		Other	Unknown	Natural Habitat	0	0

Permits

Provisos

Proviso:
Animal numbers are not shown on this approval certificate, as the approved animal numbers are provided under CA 2014/10/817 DAFF AEC Approval.
This certificate is to show that the project has been ratified by a University of Queensland AEC.

Approval Details

Description	Amount	Balance
Rabbits (Unknown, Other, Natural Habitat)		
19 Nov 2014 Initial Approval	0	0

Animal Welfare Unit
UQ Research and Innovation
The University of Queensland

Cumbrae-Stewart Building
Research Road
Brisbane Qld 4072 Australia

+61 7 336 52925 (Enquiries)
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+61 7 336 52713 (Coordinator)

animalwelfare@research.uq.edu.au
uq.edu.au/research