Modelling the spatial spread of Japanese knotweed (Fallopia japonica) in the United Kingdom

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Modelling the Spatial Spread of Japanese Knotweed (*Fallopia japonica*) in the United Kingdom

by

JAMES MARTIN DEREK SMITH

A Doctoral Thesis

Submitted in partial fulfilment of the requirements for the award of

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June 2006

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Abstract

*Fallopia japonica* (Houtt. Ronse Decraene) (syn *Reynoutria japonica* syn *Polygonum cuspidatum*, Japanese knotweed) is an aggressively invasive alien weed in the United Kingdom (UK) and throughout its introduced range. Its presence can herald considerable costs, both in terms of its ecological impact as a threat to biodiversity and economically due to the physical damage caused to property and the associated costs of treatment and disposal of the plant. There is, therefore, increasing interest in eradicating this alien species and as a result many different management techniques have been applied to try and control its spread. It is important to ascertain which of these are most appropriate in any given situation and so tools that can test the impact and efficiency of these techniques both quickly and cheaply would be extremely useful.

In this thesis mathematical models are developed for the spatial spread of *F. japonica* on a local scale in the UK. Previously, little work has been undertaken for this problem. Existing models for the plant in its native range are not directly applicable to the UK invasion due to large differences in the behaviour of the plant in the differing locales and the work that does exist for the domestic problem tends to focus on a regional, national or continental scale. It is, however, at the local scale that modelling of the spread of *F. japonica* would be of most use to many of the parties affected by its presence. Thus, the primary aim of this thesis is to develop stochastic and deterministic local-scale models that can predict the spread of *F. japonica* for stands that are free of antecedent management. These may then serve as a basis for more detailed models incorporating management techniques such as herbicides and biocontrol agents.

Parameterisation of the models is achieved via extraction and analysis of data from fieldwork, the results of which are also used for simulation output validation. The fieldwork itself and the results thereof are described herein. A stochastic 3D correlated random walk model for the development of the subterranean rhizome network of a single stand of *F. japonica* is then developed, simulations of which allow us to investigate the importance of various parameters in affecting crown density and rates of stand expansion. The correlated random walk model predicts quadratic growth in time of the stand area, motivating the use of a 2D Fisher model as a phenomenological representation of the spread of aerial stems. Finally, the effects of a watercourse on spatial spread is investigated using a compartmentalised 1D model for stand growth along a riverbank and the transport of rhizome/stem fragments in the watercourse.
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Chapter 1

Japanese knotweed (Fallopia japonica)

The past is a foreign country, they do things differently there

L P Hartley, The Go-Between, 1953

1.1 Introduction

Fallopia japonica (Houtt) Ronse Decraene (Japanese knotweed) is an aggressively invasive alien weed in the United Kingdom (UK) [18, 25] It was introduced to the UK in 1825 [6, 18] from its native range in Japan and following its naturalisation in 1886 [22] the plant has become a major problem, both ecologically and economically, throughout its introduced range As such, the monitoring and prediction of its spread is of considerable interest to a number of both public and private organisations This work seeks to develop stochastic and deterministic models for the spatial spread of F japonica on a local scale in the UK In this section the plant itself is introduced along with some of its physiology, history and the problems it causes

1.2 History

Fallopia japonica is native to Eastern Asia, particularly Japan, Northern China, Taiwan and Korea [6, 18] It was first introduced to the UK from its native Japan in 1825 [18] and naturalised in 1886 [20] It is currently found over much of mainland Europe, the USA, several provinces in Canada, Australia, New Zealand and is only absent in the UK on the Orkney Islands Originally the plant was introduced to the UK for use as an ornamental
garden plant due to its attractive appearance. Later it was found that the plant’s young shoots are palatable to cattle, sheep, goats and horses and thus it was used as a fodder plant and in the USA particularly, but also elsewhere, it was used for the stabilisation of sand dunes and mine spoil. These and a number of other uses are discussed in [18], including

- *Fallopia japonica*’s height and dense clumps of shoots make it an attractive plant for screening purposes

- The Japanese eat the young shoots by stir-frying them. The Internet holds various recipes including Apple and Knotweed Pie, Knotweed Sherbert, Knot soup, Steamed Knotweed Sesame and Strawberry-Knotweed Cobbler

- In the Far East it is commonly used as a medicine for a variety of illnesses. It is also an excellent source of vitamin C and eating large quantities can have a gentle laxative effect

- Recently, it has been found that the plant contains very high levels of rezveratrol, a strong anti-cancer agent [12]

Even though it clearly has its benefits, it has been illegal to spread *F. japonica* in England since 1981 [19] because of the problems associated with its presence (see Section 1.4)

### 1.3 Taxonomy, Physiology and Morphology

*Fallopia japonica* (Fig. 11) is a member of the buckwheat family (Polygonaceae) and goes by several different names. The scientific name currently in use is *Fallopia japonica* but in the past it has had others such as *Reynoutria japonica*, *Polygonum cuspidatum*, *Polygonum steibolzi*, *Polygonum japonicum*, *Polygonum zuccharum*, *Pleuropterus zuccarznu*, and *Polysorrum reynoutra*. The Japanese call it ‘*itadon*’, meaning ‘strong plant’. *F. japonica* also has a number of different common names across its introduced range, including Sally rhubarb, huzhang, donkey rhubarb, Reynoutria, gypsy rhubarb, Hancock’s curse, Pysen saethwr, Glinc each bhwarch, Mexican bamboo, Japanese bamboo, Japanese fleece-flower, wild rhubarb and crimson beauty [18]

*Fallopia japonica* is an upright, shrub-like, rhizomatous, perennial giant herb [17]. Its stems can grow to around 3 metres in height and are bamboo-like with arching branches and sprays of small white flowers in the late summer and autumn. The stems themselves are thick, smooth and swollen where the leaf meets the stem at the joint. Leaves can grow up to 120 mm in length and can vary from a triangular to a broadly oval shape with a pointed tip [18] (Fig. 11, right)
The plant has the ability to reproduce both sexually (requiring a male and female plant) and vegetatively. However, to date all of the recorded *F. japonica* in the UK has been female [18], meaning that its primary mode of spread is via vegetative growth of the subterranean rhizome system, as well as regeneration from stem fragments [25]. Rhizomes (strictly underground stems) send out roots and shoots from their nodes and can extend up to 7 metres away from a main stand (group of individual plants growing in close proximity) and up to 2 metres deep [18], although there are many anecdotal reports of rhizomes growing as deep as 3 metres below the surface. As little as 0.7 grammes of rhizome or crown (the visible part of a rhizome from which buds erupt annually, forming clusters of aerial shoots) is enough to produce a new, viable plant in just six days [10]. It is primarily this property that has led it to become a growing problem throughout the UK, Europe, Australia, New Zealand and North America (see Section 1.4).

*F. japonica* also has a high tolerance of harsh conditions including full shade, high salinity, and drought and can survive floods and a wide range of temperatures. It is even a problem as far north as Alaska, which is known to have few other invasive species, and tends to be found near water sources, such as along streams and rivers, in low-lying areas, roadsides, and around old home sites [18]. See [6] and [18] for more detail on the physiology of the plant.

In the UK, most, if not all, of the seeds produced by *F. japonica* are of hybrid origin [18]. This is because all *F. japonica* plants in Britain have so far been found to be male sterile [20]. Hence, Japanese knotweed has attained its impressive current range purely through vegetative means [18, 20], mainly via rhizome fragments but also by cut stems [20].
1.4 Associated Problems

The problems caused by *F. japonica* are many and varied. It has been described in the past as the most invasive plant in Britain [17, 23] and damages native flora, destroys habitats, increases flood risk, causes physical damage to buildings and property, obstructs public access and even affects sites of archaeological interest [18]. The damage that *F. japonica* can cause in the UK has led to considerable interest from a wide variety of parties including councils, private landowners, property developers, and environmental groups, particularly in methods of managing the plant. On a broader horizon, its invasive nature throughout its introduced range has led to the plant becoming a problem throughout Europe, Australia, New Zealand, and North America. This has resulted in the plant having a wealth of legislation passed against it. For example, in the UK it is an offence under the 1981 Wildlife and Countryside Act to (deliberately) cause the plant to grow in the wild [18, 19].

Figure 1.2 illustrates some of the interspecific competition exhibited by *F. japonica*. The plant's tall bamboo-like stems grow to their full height of 2–3 m in a single growth season [18]. During the winter, these stems die, leaving the dead stem standing or lying on the floor. This debris can take up to three years to decompose but during this time it is reinforced by the dead canes of subsequent years, building a thick layer of decaying matter on the ground. Additionally, the annual new stems mingle with the old dead stems that have yet to fall to form dense thickets that compound the crowding out of other species. This effect is further enhanced by the zig-zag formation of its leaves which maximizes the light it receives from the Sun but produces a dense canopy under which few competing species can survive [6]. This is also mentioned in Talmage and Kiviat [55] who state, for an infestation in the USA, that

On extensive reaches of the Batavia Kill (e.g., generally in the Windham to Ashland section), Japanese knotweed covers extensive areas of the banks and the floodplain as well as smaller patches in the streambed. Knotweed has altered the distribution and development of riparian plant communities.

Besides this threat to indigenous plant life, local wildlife also suffers as their natural habitats are crowded out by *F. japonica* and thus it presents a serious threat to biodiversity.

Since the plant is not a native of the UK, it has few predators and pathogens associated with it [18], including no parasitic nematodes, no parasitic fungi and no recorded diseases [6]. This has meant that, with little competition for resources, it has become an aggressive and successful invader of the British countryside and urban areas alike. Because there is little to impede its growth, it is able to grow to a far greater size than its counterparts in Japan who have every part of their structure under attack from various insects, fungi and
pathogens. In fact is it rare to see an undamaged leaf in Japan (see [4]).

As well as the ecological costs imposed by the spread of *F. japonica*, it is also of considerable economic cost in terms of physical damage, management and disposal. *F. japonica* can cause damage to paving and tarmac, flood defence structures, archaeological sites, roads, and homes; it can reduce land prices because of the difficulty associated with removing it once it has become established; dead stems washed downstream in watercourses present an increased risk of flooding and removal of waterside infestations can mean that there are no other plants on the banks to reinforce their integrity, thereby making soil erosion easier.

Careful and considered management of the plant is therefore essential (see Section 1.5), but the costs of management can be prohibitively large. For example, for a county council in Wales, UK, the estimated annual cost of management was £300,000 in 1994. See [18] for more details on economic costs. Section 3.5 details a case study in which the future costs of disposal of contaminated soil are estimated based on model predictions.

### 1.5 Management Techniques

The negative impacts of the presence of *F. japonica* affect a wide variety of parties including those involved in nature conservation, recreational and landscape development, river management and maintenance, and property developers [18]. As a result, various different management techniques have been applied to try and control the spread of the plant including:
• Mowing stands with a standard grass-mower can be quite an effective means of controlling *F. japonica* as long as the mowing is regular and cut stems are disposed of correctly after cutting [18]. Flailing is not recommended, however, since it can result in further spread of the plant through small cut pieces being strewn about the immediate vicinity.

• Manual pulling up of shoots can be very effective where other methods of control are impractical. If kept up for 3 or more years, pulling mature stems from the base complete with roots can completely kill small patches [18]. This method is only really suitable for small, relatively new patches that have not yet had a chance to fully establish.

• Herbicides, whilst being highly successful, do have restrictions on their use. Much legislation exists on the type of herbicide that may be used in specific target areas. Health and safety legislation, proximity to water-courses, the sensitivity of a site (e.g., nature reserve) and the need to replant on the site afterwards all present problems for choosing the right herbicide [18].

• Grazing as a method of control is not quite as effective as some of the other methods. The plant used to be used as fodder since the young shoots are quite palatable to livestock. Thus, grazing may be used as cheap management, so long as it is kept up throughout the growing season. However, even intensive grazing will not eradicate the plant but only suppress it [18].

• Biocontrol presents perhaps the most interesting and potentially effective management technique. In its native range, *F. japonica* comes under attack from many different pathogens, invertebrates and nematodes, but in the UK it has few natural enemies. Biological control would involve importing one of its natural enemies for release in its introduced range. Whichever species is eventually selected as the one for release will have to pass many strict quarantine and effect tests. The successful candidate will be monophagous (meaning that it will only feed on a single type of food), thereby minimising damage to indigenous species from what could otherwise potentially be another invasive pest. However, if successful, the biological control agent that is deemed most suitable could come with a variety of advantages over other management techniques [41].

  - It is relatively cheap since once the agent is released it needs no further upkeep or input other than time.
  - There is no use of man-made chemicals that may have undesirable consequences for the surrounding ecosystem.
- The initial release results in a permanent and continuous attack on the plant and is therefore indefinitely sustainable.
- The agent will be able to locate and affect most of the populations of *F japonica* in the UK automatically.
- There is no need for relanscaping following treatment as there may have been in the case of digging and chemical use.

Biocontrol does have some disadvantages though in that it may not get rid of all of the weed and may only be effective in reducing it to acceptable levels. It can also take 5-10 years to see the desired effects so the timescale is an important factor.

- Ineffective management methods include burning and deep-digging. The latter can actually be responsible for considerable increases in stem density if not coupled with simultaneous herbicidal treatment [18]

The effectiveness of these management strategies can vary considerably, from killing a stand (e.g. herbicides) to actively assisting its dispersal or encouraging denser shoot growth (e.g. flailing) [18]. Each of these techniques also has its own costs and viabilities to consider, an example of which are the herbicides which can only be used in certain locations or conditions. See [18, 19, 20] for more details on management techniques.

In Swansea, Wales, *F japonica* is a major problem and the City and Council of Swansea established a strategic action plan in 1997 in order to deal with it [32]. A comprehensive ground survey was carried out in the city and surrounding area in 1992 and again in 1998 to obtain a clear idea of the extent of the problem. The results of these surveys were transferred to a Geographical Information System (GIS), thereby facilitating interpretation of the data and allowing various links to be made between different aspects and issues associated with the presence of *F japonica*. See [16, 19, 32] for more information on the use of GIS. Some of the data from these surveys were to be used in the motivation of this work and as potential benchmarks for use in the validation of simulation output (see Section 4.4). This is discussed later in the text.

### 1.6 Motivation for Modelling

Despite the serious problems *F japonica* can create (see Section 1.4), funding for the treatment of sites infested with *F japonica* remains difficult to obtain, as illustrated by the following example.
Here [Washington State, USA], much of our concern about knotweed has been focused on riparian areas. One of the many reasons for this is political. Salmon are one of the icons of the Pacific Northwest that has nearly achieved deity status. Huge amounts of money and political will has been spent on protecting this species and others like it. One of the main sources of funding for habitat work in Washington State has been the Salmon Recovery Fund (SRF, pronounced surf, Board). This funding has been virtually closed to invasive species work. Although the SRF board strongly supports the concept of LWD [Large Woody Debris] in streams and seems to understand the need to protect riparian vegetation, they fail to see a connection of huge monocultures of knotweed along with the river banks to what is happening in a stream. Frankly, one of the biggest problems I see is that although knotweed may grow within groves of alders, there are no seedlings, or really any plants underneath the knotweed. I feel the most significant ecosystem impacts of knotweed are yet to be felt.

*Cathy Lucero, pers. comm*

There also exists a need to promote the consequences of procrastination to owners and developers of land in the timely removal of an infestation from their property. Thus, a tool that could demonstrate the future costs of not treating these sites immediately by illustrating the plant’s aggressive spread or assess the effects of the various management techniques (see Section 15) would be widely welcomed in the promotion of the problem and the prioritisation of sites for treatment. In this study the basis for such work is built by carrying out fieldwork to gather relevant information on the plant and creating models based on the resulting data for the spatial spread of unmanaged stands of *F. japonica* in the UK.

There exists a large amount of literature on *F. japonica*. Specific areas covered include its reproductive strategies and capabilities [6, 9, 10, 25, 27, 38, 49], management techniques and their effectiveness [8, 16, 19, 20, 24, 30, 32, 51], the importance of scale in the interpretation of distribution maps and model output [21, 40, 56], its effects on riparian habitats [24, 50, 57], nitrogen uptake and use [15, 34, 35, 36, 37], and its genetic makeup and hybridisation [6, 39, 43]. There is also a growing amount of data on the distribution of the plant throughout the British Isles collected for or by groups such as the City and Council of Swansea, the Cornwall Knotweed Forum and the Environment Agency. However, despite increasing interest and literature on the plant, there are few papers on modelling the spatial spread of *F. japonica*. Most of these are concerned its advance on a regional, national or continental scale (see, for example, [5, 7, 21]). There seems to be only one example of modelling the spread on a local scale, namely Adachi *et al.* [3], yet it is at this scale that the modelling would be most useful to many interested parties. Adachi *et al.* construct a two-dimensional stochastic model for
the development of a rhizome network in Japanese plants in their native range. Their model is similar in principle to the one presented in Chapter 3 and uses field data gathered from the slopes of Mount Fuji to build a model based on a number of iterated rules. However, there are a number of issues that somewhat limits the applicability of Adachi et al.’s model to *F. japonica* in the UK.

1. The work of Adachi et al. was based in Japan on *Reynoutria japonica* (syn. *F. japonica*) that was actually closer in nature to *F. japonica* var. *compacta* [1], the morphology and physiology of which contrasts markedly to the *F. japonica* var. *japonica* considered in this UK study.

2. The field work upon which their model is based was carried out on the slopes of Mount Fuji, at a much greater altitude than the *F. japonica* found in the UK. Bailey [4] has shown that altitude affects the plant’s growth significantly, particularly due to a contraction of the growth period in Japan. Additionally, the soil on Mount Fuji consists mainly of volcanic ash and there is a much greater incidence of predation from invertebrates, such as chrysomelid beetles, sawfly and Japanese swift moth larvae [4], and fungi such as some *Puccinia* species and *Phyllosticta rapae* [18]. This means that the environmental conditions in Japan are more harsh than the climate and terrain in the UK.

3. The size of the plant and its growth habit in the UK differ to those in its native range. In Britain and Northern Europe *F. japonica* stems may grow up to 3 m tall and form densely packed crowns at their base. However, Japanese stands tend to consist of sparse, single, much shorter stems [4].

4. A key feature of Adachi et al.’s model is the formation of central die-back as the plant grows, forming a rough annulus of aerial stems, this feature has not been recorded in UK plants. Adachi et al. [2] conclude that this central die-back is primarily driven by the growth pattern of the rhizome system. However, it is well-known that crowns in the UK have a lifespan that far exceeds the 5 years assumed in Adachi et al.’s work (one possible explanation for the lack of central die-back formation). It is clear that the UK *F. japonica* rhizome networks develop differently to those of Adachi et al.’s *R. japonica*.

5. Data from this study shows that not every rhizome of the UK strain produces a crown.

6. Rhizome segments in the UK are not straight, as assumed in Adachi et al.’s model. Extreme changes in direction may be observed in very small sections of a segment (see
7. The rhizomes grow up to 2 m deep [18] and, according to anecdotal reports, sometimes even deeper which is one reason why the plant is so difficult to control. Rhizomes are known to grow underneath walls and building foundations causing damage to property. This means that a two-dimensional model such as that proposed by Adachi et al. is limited in its usefulness and is the main reason why a three-dimensional approach to modelling the rhizome network is adopted in Chapter 3.

Figure 1.3: An example of the extreme changes possible in the direction of growth of a rhizome segment. Image width approximately 15 cm.

Given the differences in the plant’s behaviour between its native and introduced range, it is necessary to construct models that are more relevant to the conditions and plant physiology found in the UK. In this report the models focus on the spatial spread of unmanaged stands of *F. japonica* to form the basis of potential future models that might incorporate the various management techniques, for example, to facilitate the prioritisation of sites for treatment or demonstrate to landowners the consequences of procrastination when deciding whether treatment is required. Like Adachi et al., the modelling initially focuses on the growth of the subterranean rhizome network since the location and spread of the aerial shoots is a direct consequence of the development of this network. However, in order to do so it is necessary to have a thorough understanding of the network’s morphology and physiology. At present there exists very little data on the behaviour of the rhizomes beneath the soil besides work on genetics and chemical content, yet the ‘clonal growth parameters’ (rhizome segment lengths, branching angles and number of daughters) have a critical impact on the way in which rhizomatous plant species grow in terms of size and shape [13]. It was therefore necessary
to obtain some field data for use in the parameterisation of the models. The collection and analysis of field data is discussed in Chapter 2 and a correlated random walk model for the development of the rhizome network that uses much of the obtained field data is then discussed in Chapter 3. In Chapter 4, a simulation of a reaction-diffusion model for the spatial spread of the aerial stems is constructed and the influence of watercourses on observed spread rates is investigated via a 1D model of stem spread along a riverbank. This bankside model is then incorporated into the original 2D simulation to illustrate the effects of riparian habitats on the spatial spread of *F. japonica*. Finally, conclusions and future work are discussed in Chapter 5.
Chapter 2

Fieldwork

Nihil est in intellectu quod non fuit prius in sensu [Nothing is in the understanding, which was not first perceived by some of the senses]

John Locke

2.1 Introduction

A major prerequisite for modelling a biological process is a detailed qualitative understanding of the process itself and also of the internal and external factors affecting it. In this case it is known that although *F japonica* is functionally dioecious and is able to reproduce sexually in its native habitat, to date all of the recorded plants in the UK have been female [18]. It has therefore achieved its current distribution via vegetative growth alone. As such, the rhizome network of a stand plays an essential role in its dispersal strategy and understanding the development of such a network is key to any modelling. Furthermore, a model that seeks to represent the biology as accurately as possible will also require considerable quantitative knowledge about the various aspects of the subject. This facilitates the parameterisation of the model with relevant, empirically-obtained parameter values as well as the validation of the model itself.

Prior to this work, there exists very little data on the morphology of the rhizome networks for *F japonica* in the UK beyond that discussed in Section 1.3. Indeed, the only example found of such data from further afield was that of Adachi *et al* [2, 3]. Fieldwork was undertaken on two separate sites to gather such data and to investigate various aspects of the plant and the structure of the rhizome network. For the results to be valid it was required that the stand be situated in a representative environment and be free of the influences of management, as discussed in Section 1.5, some management techniques can actually assist the development of the plant if not applied correctly or if application is terminated prematurely.
In this chapter, the fieldwork is described, results are discussed and some inferences about the way in which the network develops are made.

2.2 Survey 1

The first survey was carried out on the 23rd February 2004. The purpose of this fieldwork was to find out as much as possible about the structure of the rhizome network and to try and understand the manner in which it grows. A number of surface measurements were also taken. This work was carried out with the assistance of Dr Lois Chl1d of the Centre for Environmental Studies at Loughborough University and James Macfarlane of Cornwall County Council.

Some of the relevant questions and data sought included:

- Segment lengths: A segment length distribution is a key component of the correlated random walk model (to be discussed in Chapter 3).

- Branching angles: A probability distribution for the selection of branching angles is another key component of the correlated random walk model.

- Position of shoots/buds: Where do stems shoot from? Is it at the apex of a rhizome segment (as assumed in Adachi et al.'s model [3]) or somewhere along its length?

- Maximum length of rhizomes: An upper limit on the total length of a rhizome, inclusive of all of its constituent segments.

- Crown separations: This includes both nearest-neighbour and trans-network separations.

- What is the maximum depth at which shoot growth occurs?

- How many daughter rhizomes does each primary rhizome have?

- What is the maximum branching order of the segments as measured from their parent crowns?

- Is segment length correlated with branching order or directly-connected segments? Adachi et al.'s model (see [3]) assumes a linear increase in segment length with branching order.
• Is it possible to gauge the age of rhizome segments, for example by counting the different-coloured rings in a rhizome cross-section in a similar way to the annual rings in a tree?

• How do different order rhizome samples compare in age/shape/colour/size of core/rings and so on?

• How does the spatial distribution of new shoots look?

• How important is apical dominance in controlling branching or crown formation events?

• Is there a relationship between branching angles and segment diameters?

2.2.1 The Site

<table>
<thead>
<tr>
<th>General Site Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>O.S. National Grid Reference</td>
</tr>
<tr>
<td>Location</td>
</tr>
<tr>
<td>Longitude</td>
</tr>
<tr>
<td>Latitude</td>
</tr>
<tr>
<td>Altitude</td>
</tr>
<tr>
<td>Habitat Type</td>
</tr>
<tr>
<td>Soil Type</td>
</tr>
<tr>
<td>Approx. Stand Area</td>
</tr>
</tbody>
</table>

Table 2.1 General site information for the first survey

A site in Penhallick, Cornwall (see Table 2.1) was chosen for the first survey from a number of possible candidates. The site consisted of a large stand of *F. japonica* (approximately 200 m² in area) in a woodland habitat a few metres behind a road verge (Figure 2.1, left). It contained a dense thicket of old, dead canes from previous years and abundant evidence of new shoot growth from that year's growth season. The characteristic bright-red/pink buds and shoots, ranging from ground level to over 30 cm in height, could be seen throughout the stand. Identification of crowns was relatively difficult due to the many dead stems already having fallen and, despite the stand being at least 25 years old, few very large crowns were found. Instead, it seemed that the stand was mainly formed of a large number of smaller crowns, interspersed with individual stems. Within the stand, a number of associated plant
species were present including Hemlock Water Dropwort (Oenanthe crocata), Hart’s Tongue Fern (Phyllitis scolopendrium), Ivy (Hedera helix) and Hard Fern (Blechnum spicant).

The specific area designated for rhizome extraction was a smaller zone on the periphery of the main stand (Figure 2.1, right), consisting of several smaller crowns that were thought likely to be interlinked by a continuous and traceable rhizome network. This precise location was chosen primarily for its ease of access and natural drainage facility due to the ground lying on a reasonable gradient. This was important for the extraction technique employed (see Section 2.2.2). The topsoil was a loam (soil consisting of a mixture of sand, clay, silt or organic matter) but buried within it was a large quantity of slate, rubble, bottles, domestic china and a variety of metallic objects. This suggests that the stand may well have originated from some dumped household material, a common find in infested areas.

2.2.2 Methods

Given the limited time available for work on-site, in situ measurements of the rhizome network were unfeasible. Work therefore consisted of precursory surface measurements and the rhizome extraction itself. Samples were then taken back to the laboratory for further investigation.

Surface Measurements

Prior to any rhizome extraction a number of surface measurements were taken from the main stand. Firstly, three distinct quadrat surveys were taken from different parts of the main
stand (see Figure 2.2) in order to investigate the spatial distribution of new shoots. Each quadrat (1 m x 1 m) was thrown on to the ground at random locations within the boundaries of the stand, the surface litter cleared, and the number of new shoots present within the quadrat and their coordinates with respect to the quadrat frame were recorded. New shoots from pink/red buds at surface level up to those that were over 30 cm tall were included in the count.

![Figure 2.2: One of the quadrat surveys taken.](image)

Table 2.2 shows the data recorded during the quadrat surveys. The three samples yielded a mean distance to the nearest neighbouring shoot of 10.88 cm, with a standard deviation of 7.08 cm. The separations were therefore highly variable with some shoots closely clustered and others less so. Figure 2.3 illustrates graphically how the new shoots were distributed within the quadrat samples. It is unclear from these surface measurements whether nearby shoots are closely connected by the rhizome network or not.

Figure 2.4 shows the frequency distribution of the distance of each new shoot to its nearest neighbouring shoot. The majority of new shoots are typically formed very close to one another, being within 15 cm of each other. Since crown separations are known to be much larger than this (see Fig. 2.5 and Section 2.3), this confirms that not every new shoot will go on to form a crown. This is thought mainly due to intraspecific competition but may also in part be due to such external factors as weather-induced mortality.

A line transect of 10 m in length was taken at a random location within the boundaries of the main stand. It was assumed that the stems from the previous year could be distinguished from new growth by their mature appearance, texture and height and from older remaining stems by their darker colour and residual suppleness indicative of lower levels of decomposition. The distances along the transect of individual stems from the previous
<table>
<thead>
<tr>
<th>Sample Number</th>
<th>Distance to Nearest Neighbour (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Quadrat</td>
</tr>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>4.243</td>
</tr>
<tr>
<td>2</td>
<td>4.243</td>
</tr>
<tr>
<td>3</td>
<td>5.000</td>
</tr>
<tr>
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<td>8.246</td>
</tr>
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<td>5</td>
<td>12.309</td>
</tr>
<tr>
<td>6</td>
<td>3.162</td>
</tr>
<tr>
<td>7</td>
<td>3.162</td>
</tr>
<tr>
<td>8</td>
<td>12.207</td>
</tr>
<tr>
<td>9</td>
<td>3.606</td>
</tr>
<tr>
<td>10</td>
<td>21.633</td>
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<tr>
<td>11</td>
<td>15.133</td>
</tr>
<tr>
<td>12</td>
<td>3.606</td>
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<tr>
<td>13</td>
<td>20.224</td>
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<tr>
<td>14</td>
<td>20.224</td>
</tr>
<tr>
<td>15</td>
<td>24.207</td>
</tr>
<tr>
<td>16</td>
<td>24.207</td>
</tr>
<tr>
<td>17</td>
<td>10.630</td>
</tr>
</tbody>
</table>

| Mean Distance to Nearest Neighbour | 10.8834 cm |
| Median Distance to Nearest Neighbour | 10.4403 cm |
| Standard Deviation                  | 7.0833 cm |

Table 2.2 Data from the quadrat survey
Figure 2.3 Maps of the quadrat survey results showing the coordinates (cm by cm) of the new shoots measured relative to the quadrat frame.

Figure 2.4 The frequency distribution of nearest neighbouring new shoot separations.
year within 1 m perpendicular to the transect were then recorded (see Table 2.3). Similar measurements were made for existing crowns with the additional data on their approximate dimensions and the number of constituent stems from the previous growth season present (see Table 2.4).

<table>
<thead>
<tr>
<th>Stem number</th>
<th>Distance along transect (cm)</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>40</td>
</tr>
<tr>
<td>2</td>
<td>55</td>
</tr>
<tr>
<td>3</td>
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<td>4</td>
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<td>490</td>
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<td>13</td>
<td>730</td>
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<tr>
<td>14</td>
<td>760</td>
</tr>
<tr>
<td>15</td>
<td>900</td>
</tr>
<tr>
<td>16</td>
<td>910</td>
</tr>
</tbody>
</table>

Table 2.3 The distances along a 10 m line transect that stems from the previous growth season were recorded.

Figure 2.5 illustrates the area on the periphery of the main stand from which rhizome samples were taken. Nearest-neighbouring crown separations were measured, along with the height attained by the old stems.

**Rhizome Network Extraction**

In order to obtain as much information about the structure of the rhizome network, a large area on the periphery of the main stand (see Fig. 2.5) was unearthed such that network samples could be extracted without damaging the fragile rhizomes where possible. The use of a mechanical digger or spades and shovels presented considerable risk of damaging the network and so the removal of topsoil was achieved via the novel method of washing layers of soil away with an industrial pressure-washer (Fig. 2.6, left). Once the surface litter and vegetation had been removed, the natural gradient of the site provided drainage for excess...
<table>
<thead>
<tr>
<th>Crown number</th>
<th>Distance along transect (cm)</th>
<th>Stems from previous year</th>
<th>Approx. crown dimensions (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>118</td>
<td>9</td>
<td>48 x 60</td>
</tr>
<tr>
<td>2</td>
<td>300</td>
<td>8</td>
<td>40 x 43</td>
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<td>3</td>
<td>430</td>
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<td>30 x 30</td>
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<td>580</td>
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<td>46 x 26</td>
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<tr>
<td>6</td>
<td>673</td>
<td>4</td>
<td>9 x 10</td>
</tr>
</tbody>
</table>

Table 2.4 Distances of crowns along the line transect, their approximate dimensions and the number of stems from the previous growth season on each crown.

Figure 2.5 An illustration of the area designated for rhizome extraction. Crown 0 is the oldest crown in the chain and connects to the main stand as shown by the dotted line. Single shoots are marked with an 'X' and the feathered arrows mark the downhill direction. Distances of nearby crowns (A–J) were 0.45 m, 0.40 m, 0.27 m, 0.80 m, 0.40 m, 1.60 m, 1.60 m, 0.60 m, 1.00 m, 0.90 m respectively. A–J also represent the network’s connectivity. Heights of the previous year’s stems ranged from 1.3–2 m.
water and this method proved very effective at exposing rhizomes with minimal damage (Fig. 2.6, right).

![Figure 2.6: Removal of topsoil using a pressure-washer (left) and soil cleared to a depth of around 30 cm, exposing a portion of the rhizome network (right).](image)

Although it was not possible to extract the whole network intact, a few large sections of it and many smaller samples were obtained (Fig. 2.7). These were labelled, their interconnectivity recorded where possible and the samples were bagged to be taken back to the lab for cleaning and measurement. Soil was removed by bathing the networks in water to loosen the compacted soil and then brushed lightly with a toothbrush for finer cleaning.

![Figure 2.7: An example of a small part of the network extracted.](image)
2.2.3 Results

Following the cleansing of samples, the morphological properties of the networks were examined. The distinct sections of the network were pieced together where possible and the relationships between interconnected segments were recorded. This was achieved via the identification of a ‘parent’ segment and its progeny, the ‘daughter’ and ‘continuation’ segments (see Fig. 2.8). Hereafter, the terminology ‘rhizome’ refers to a complete rhizome from its base to its tip inclusive of all of its related continuations (a + b in the diagram) whereas a ‘segment’ refers to a single section of a rhizome (a, b or c in the diagram) between branching points or a branching point and terminus.

![Diagram of rhizome relations](image)

Figure 2.8 Rhizome relations. Here, the ‘parent’ segment (a) is produced by the crown, the ‘continuation’ (b) continues in roughly the same direction as the parent following the branching point, and the ‘daughte’ segment (c) branches off of the parent at the branching point.

It was assumed that the crown directly connected to the main stand (Crown 0 in Fig. 2.5) was the oldest and hence the source of the entire studied network. This idea was supported by the much larger diameter in the segment connecting to the main stand and serves as a basis for deciding on the branching order for each segment (see below). The remaining crowns were found to be interconnected in the manner depicted in Fig. 2.5.

Subsequent data obtained (see below for more detail) included:

- Crown number
- Reference number
- Relationship to predecessor
- Trace code
- Generation of segments
- Segment lengths
- Branching angles
• Internode lengths
• Diameter of segments
• Depth of segments
• Number of buds on the segments.
• Bud separations
• Crown diameters
• Number of old shoots on crowns
• Distance between shoots on a crown and their nearest neighbouring shoot
• Number of buds on crowns

Crown number
This represents a reference number recording which crown each segment directly or indirectly originates from. These correspond to the numbers given in Fig 25. Nine distinct crowns were recorded in the subject area.

Reference number
A reference number assigned to each rhizome segment purely for administration purposes.

Relationship to predecessor
Where possible, each segment was labelled as a ‘parent’, ‘continuation’ or ‘daughter’ as described above. This was important for the assignment of a trace code (see below). Whilst this was trivial for those samples which could be traced directly back to their parent crown, some segments and small networks were impossible to trace fully. In this case, an estimation was made as to their relationship to connected segments by examination of associated branching angles and rhizome thickness. Additionally, some segments were both daughters as well as parents, in which case they were labelled as daughters to facilitate the assignment of a trace code.
Trace code

The formulation of the trace code was essential in the reconstruction of the network. This code takes the form ‘1Fx’ or ‘2Fx’ which is read as ‘the first (or second) segment following a branching point from the segment with reference number x’. Thus, a segment assigned a trace code is either a continuation or a daughter segment. When coupled with the ‘relationship to predecessor’ data the lineage of a segment may be traced and the network reconstructed.

Generation of segments

The ‘generation’ (branching order) of a segment was assigned according to a modified Gravelius ordering scheme. The Gravelius ordering scheme is used in the ordering of stream networks and biological branching networks (see [46]). Here, a ‘primary’ segment is defined as one that has its base at a crown meaning that it was produced by the crown rather than generating the crown itself. Then, primary segments are the first generation, their continuations are also first generation and their daughters are considered second generation. Thus, the crown represents the ‘source’ rather than the ‘mouth’ as would be the case in stream networks and is equivalent to the ‘root’ in tree structures. This is illustrated in Fig. 2.9.

![Figure 2.9](image-url)  
Figure 2.9 The modified Gravelius ordering system. Black circles represent rhizome tips and branching points. The numbers shown denote the segment’s ‘generation’ (branching order).

The branching order was not found to exceed the third generation in this study. However, this may be an artifact of the relatively small sample set.
Segment lengths

Segment lengths are defined as the distance along the segment from the base (or a branching point) to the tip or the next branching point. Table 2.5 details some statistics for the segment length data.

<table>
<thead>
<tr>
<th>Segment Lengths</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Samples</td>
</tr>
<tr>
<td>Mean</td>
</tr>
<tr>
<td>Modal Group</td>
</tr>
<tr>
<td>Mode</td>
</tr>
<tr>
<td>Skew</td>
</tr>
<tr>
<td>Kurtosis</td>
</tr>
<tr>
<td>Standard Deviation, $\sigma$</td>
</tr>
<tr>
<td>Minimum</td>
</tr>
<tr>
<td>First Quartile</td>
</tr>
<tr>
<td>Median</td>
</tr>
<tr>
<td>Third Quartile</td>
</tr>
<tr>
<td>Maximum</td>
</tr>
<tr>
<td>Range</td>
</tr>
<tr>
<td>Interquartile Range</td>
</tr>
</tbody>
</table>

Table 2.5 Segment length statistics

Figure 2.10 shows the relative frequency distribution of segment lengths from this study. Direct comparison with those from the work of Adachi et al. [3] is not possible in this case since a segment length in their work refers to the length of a rhizome from base to tip. This is inclusive of all of those segments that are, in this study, called 'parent' and 'continuation' segments and are considered individually here. The discrete distribution shown may be closely represented in the least squares sense by the continuous function $y = 64.31 e^{-0.0845x}$ ($R^2 = 0.9885$) where $y$ is the relative frequency and $x \in [2.5, 82.5]$ is the segment length (cm). Whilst the maximum segment length observed was 81.1 cm, it is clear from Fig. 2.10 that segment lengths tended to be much shorter than this in general with about 95% of the data within the 0.6-41 cm range and a modal group of 0-5 cm.

Figure 2.11 shows the scatter graphs parent segment lengths against that of their continuations and daughter segments. A Pearson product moment correlation coefficient (PPMCC) of 0.1991 suggests that there is no significant linear relationship between the length of parent segments and their continuations. Also, a $\chi^2$ test for independence ($p < 0.05$) between the parent segment lengths and that of the continuations yields $\chi^2 = 6.8717$ (4 degrees of freedom), meaning that the null hypothesis that there is no dependence in segment lengths.
on whether the subject is a parent or continuation is accepted. Similar comparison of parent and daughter lengths shows a PPMCC of 0.0649 so neither is there a linear relationship here. However, a $\chi^2$ test for independence between the segment lengths of parents and daughters with $p < 0.01$ yields $\chi^2 = 27.5739$ (7 degrees of freedom), meaning that statistically there is almost certainly some dependence exhibited. This is demonstrated in the mean segment length that of the daughters (17.73 cm) is larger than that of the parents (10.5 cm), and is also supported by the work of Adachi et al. [3] who include longer segment lengths with increasing branching order in their model. This feature of the morphology could be incorporated into the model described in Chapter 3 by having separate distributions from which segment lengths may be drawn for given branching order. However, it is not included in this case due to lack of information for the higher branching orders. Instead, the selection of segment lengths in the model is considered as a series of random draws from the frequency distribution shown in Fig. 2.10.

**Branching angles**

Branching angles are defined as the smallest angle formed at the base of a daughter rhizome between it and the continuation of the parent. This was measured by using a protractor where possible or an estimation by eye where the vertex was too inaccessible. Table 2.6 details some statistics for the branching angle data.

Figure 2.12 shows the relative frequency distribution of branching angles from this study and compares them with those from the work of Adachi et al. [3]. It is not clear how their data was measured so care must be taken with direct comparison. It is clear that there is considerable contrast between the two data sets. Data from this study shows a much greater
Figure 2.11: Scatter plots of parent segment lengths and their corresponding continuation lengths (left) and daughter lengths (right).

<table>
<thead>
<tr>
<th>Branching Angles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Samples</td>
</tr>
<tr>
<td>Mean</td>
</tr>
<tr>
<td>Modal Group</td>
</tr>
<tr>
<td>Mode</td>
</tr>
<tr>
<td>Skew</td>
</tr>
<tr>
<td>Kurtosis</td>
</tr>
<tr>
<td>Standard Deviation, $\sigma$</td>
</tr>
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<td>Minimum</td>
</tr>
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</tr>
<tr>
<td>Maximum</td>
</tr>
<tr>
<td>Range</td>
</tr>
<tr>
<td>Interquartile Range</td>
</tr>
</tbody>
</table>

Table 2.6: Branching angle statistics.
incidence of smaller branching angles than that of Adachi et al. [3] with around half the ratio of angles in the 30-50° range. Also of note is the large number of 90° branching angles found in this study.

![Branching Angles](image)

**Figure 2.12** Relative frequency distribution of branching angles. Data from this study (black) is compared with that of the work of Adachi et al. [3] (grey) for *Reynoutria japonica* in Japan.

Selections of branching angles in the model described in Chapter 3 are considered as a series of random draws from a frequency distribution such as in Fig. 2.12

**Internode lengths**

The nodes are the often slightly enlarged, knotty parts of the rhizome at which buds may form and develop into new rhizome branches or new aerial shoots. They are similar in appearance to the nodes found on the aerial stems. The internode length is the distance along the segment between two neighbouring nodes (see Fig. 2.13). Table 2.7 details some statistics for the internode length data and Figure 2.14 shows their relative frequency distribution.

A PPMCC of 0.1242 suggests that there is no significant linear correlation between the internode length and diameter of the segments. In fact, it is clear from observation that internode lengths can vary considerably from one internode to the next with little consistency. If the assumption that thicker rhizomes are generally older holds (see below), this suggests that internode length is not dependent on the age of the segment and hence that internodes do not continuously extend throughout the lifespan of a rhizome (see also Section 2.3.3). It is possible that the variability of internode lengths may be due to periods of faster growth, perhaps in times of higher productivity.
Figure 2.13: This section of rhizome shows the internodes (length of rhizome between nodes) marked by the arrows. Also visible are a few buds located at certain nodes.

<table>
<thead>
<tr>
<th>Internode Lengths</th>
<th></th>
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<tbody>
<tr>
<td>Number of Samples</td>
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<tr>
<td>Mean</td>
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<tr>
<td>Modal Group</td>
<td>1-1.5 cm</td>
</tr>
<tr>
<td>Mode</td>
<td>2 cm</td>
</tr>
<tr>
<td>Skew</td>
<td>1.28</td>
</tr>
<tr>
<td>Kurtosis</td>
<td>2.70</td>
</tr>
<tr>
<td>Standard Deviation, $\sigma$</td>
<td>1.17 cm</td>
</tr>
<tr>
<td>Minimum</td>
<td>0.3 cm</td>
</tr>
<tr>
<td>First Quartile</td>
<td>1.2 cm</td>
</tr>
<tr>
<td>Median</td>
<td>1.9 cm</td>
</tr>
<tr>
<td>Third Quartile</td>
<td>2.6 cm</td>
</tr>
<tr>
<td>Maximum</td>
<td>8.7 cm</td>
</tr>
<tr>
<td>Range</td>
<td>8.4 cm</td>
</tr>
<tr>
<td>Interquartile Range</td>
<td>1.4 cm</td>
</tr>
</tbody>
</table>

Table 2.7: Internode length statistics.
Diameter of segments and rhizome age

The average diameter of rhizome segments was measured using a pair of calipers. Table 2.8 details some statistics for the segment diameters and Fig. 2.15 shows their relative frequency distribution.

<table>
<thead>
<tr>
<th>Segment Diameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Samples</td>
</tr>
<tr>
<td>Mean</td>
</tr>
<tr>
<td>Modal Group</td>
</tr>
<tr>
<td>Mode</td>
</tr>
<tr>
<td>Skew</td>
</tr>
<tr>
<td>Kurtosis</td>
</tr>
<tr>
<td>Standard Deviation, $\sigma$</td>
</tr>
<tr>
<td>Minimum</td>
</tr>
<tr>
<td>First Quartile</td>
</tr>
<tr>
<td>Median</td>
</tr>
<tr>
<td>Third Quartile</td>
</tr>
<tr>
<td>Maximum</td>
</tr>
<tr>
<td>Range</td>
</tr>
<tr>
<td>Interquartile Range</td>
</tr>
</tbody>
</table>

Table 2.8 Segment diameter statistics

A PPMCC of 0.01423 suggests that there is no linear relationship between the length of a segment and its diameter (see Fig. 2.16). It is well known in arterial branching (see [46]) and some plant species that the branching angle is related to the diameter of the parent segment. However, a PPMCC of -0.1089 suggests that there is no strong linear correlation.
for *F japonica*

Bailey [4] states that for *F japonica* in the UK

"Nutrients are translocated to an extensive woody rhizome system that in some respects resembles a subterranean tree increasing in girth every year."

This concept was investigated in order that it might be used as a method of determining the age of rhizome samples. Examination of rhizome cross-sections reveals a dark or hollow centre surrounded by concentric circular regions that alternate in colour between orange, yellow or brown (Fig. 2.17). These were also investigated for a relationship between the number of rings and rhizome age that is analogous to the annual rings found in the trunks of arboreal trees.
Figure 2.17: Cross-section of a rhizome showing the characteristic orange and yellow concentric rings.

Rhizome samples studied were assigned an 'age rank' in which lower ranks are older than higher ranks. In most cases a reasonable assumption could be made by tracing the network back to the main stand to determine their relative age. Table 2.9 details the age ranks compared with the segment diameters and the number of concentric rings found.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Age Rank</th>
<th>Diameter (cm)</th>
<th>Coloured Rings</th>
</tr>
</thead>
<tbody>
<tr>
<td>lii</td>
<td>1</td>
<td>1.9</td>
<td>7</td>
</tr>
<tr>
<td>11i</td>
<td>2</td>
<td>1.0</td>
<td>4</td>
</tr>
<tr>
<td>64ii</td>
<td>3</td>
<td>1.3</td>
<td>3</td>
</tr>
<tr>
<td>93i</td>
<td>4</td>
<td>1.1</td>
<td>4</td>
</tr>
<tr>
<td>122i</td>
<td>Unknown</td>
<td>1.1</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 2.9: The ranked age of rhizomes and the corresponding diameters and number of concentric rings found.

For the following statistics the samples used were those in Table 2.9. It should therefore be noted that the sample size was small and results may therefore not be representative of the general population:

- A Spearman rank correlation coefficient (SRCC) of $-0.4$ for age rank and rhizome diameter suggests that there may be a weak linear relationship between the data sets. As expected, the older rhizomes tend to be the thicker ones.

- An SRCC of $-0.63245$ for the age rank and number of rings suggests an even stronger linear relationship. Here, the older rhizomes seem to possess more of the concentric
rings than the younger ones

- The strongest linear relationship is found between the diameter of segments and the number of rings they have, as evidenced by a PPMCC of 0.8348. Thicker rhizomes do indeed seem to have larger numbers of concentric rings.

Figure 2.18 shows the best least-squares fit for this third case, exhibiting a reasonably high $R^2$ value of 0.697 and hinting at a possible underlying relationship. However, as mentioned above, these results are from a small sample size. Whilst they may not be representative of the general population, they do motivate further investigation, particularly for the relationship between the age of a segment and the number of concentric rings it has. A way to gauge how long existing stands have been resident at particular sites would be extremely useful to a number of parties and would also facilitate further investigation of stand area expansion rates. This would be extremely useful for validation of the model discussed in Chapter 3.

![Figure 2.18](image)

Figure 2.18 Best least-squares fit for the number of rings against segment diameter

Figures 2.19 and 2.20 show diagrams of the cross-sections of the five rhizomes examined. It is clear to see the orange, yellow and dark orange/brown concentric circles of varying configuration in each sample. There were many inconsistencies between samples, besides the number of rings observed. Firstly, some of the samples had a small hole in the centre of the rhizome whilst others had none. Also, some of the innermost circles were yellow and some were orange. Diameters of the concentric circles varied considerably and some samples also exhibited a darker orange/brown ring.

Clearly these results suggest that there may be a relationship to be exploited between age, diameter and the number of rings, although further work is required to confirm this or otherwise.
Figure 2.19: Rhizome samples 1ii, 11i and 64ii (left to right) in cross-section. Segment diameters are not to scale but the relative widths of the concentric rings are.

Figure 2.20: Rhizome samples 93i (left) and 122i (right) in cross-section. Segment diameters are not to scale but the relative widths of the concentric rings are.
Depth of segments

Accurate and meaningful measurement of segment depth was not possible for the majority of samples due to on-site time-constraints. However, it is known that all samples were taken from the top 50 cm of soil. No rhizomes in the subject area were found to extend below this level. This may be a feature of the younger parts of the stand in that the rhizomes first fulfill an exploratory/colonisation role before the crowns become more established and rhizomes become more useful as vessels for nutrient storage and transportation.

Number of lateral buds

Rhizomes feature lateral buds along their length which can become either a new daughter branch or form new aerial shoots (Fig. 2.21). These lateral buds lie dormant under the influence of apical dominance until such time as they are activated. Auxins (growth hormones) are produced in the apex on a growing tip which simultaneously encourage the extension of the tip whilst suppressing the development of nearby lateral buds. If the apex is subsequently removed or if it grows far enough from the buds such that the levels of auxin fall below the activation threshold then a bud may be activated and begin its development into a new rhizome branch or aerial shoot. This effect is utilised in botany through pruning, topiary and bonsai to encourage plants to become ‘bushier’. Buds are found on the nodes of rhizomes and are often pink/red in colour. Those counted were exclusive of existing branching points which, although they were once buds, avoids ambiguities with regard to which segment (parent, daughter or continuation) the bud ‘belongs’ to.

Figure 2.21: A dormant lateral bud (A) and a newly activated bud forming a young shoot (B).

A mean of 10.36 buds per metre ($n = 154$) was found, but the data were highly variable
with a minimum of 0, a maximum of 166.67 and a standard deviation of 21.62. This is explained by the influence of a small number of very short segments that had a single bud on them, meaning that they predicted an artificially high number of buds per metre. Figure 2.22 shows the frequency distribution for the number of buds per metre in which it is clear that the majority of segments predicted 0–5 buds per metre. However, this is due to 90 (58.4%) of the samples not having any detectable buds on them at all. Buds generally form in the autumn in preparation for over-wintering and subsequent development of new shoots in the spring [18]. Given that this survey was undertaken in February, the lack of buds evident on so many of the samples may therefore be a product of seasonal variation in bud formation.

![Figure 2.22: Frequency distribution for the number of buds per metre (n = 154).](image)

**Bud separations**

The distance between neighbouring buds on rhizome segments was measured. A mean separation of 4.1 cm was found with a standard deviation of 5.1 cm (n = 357). The high standard deviation is explained by the influence of relatively few large separations as evident in the frequency distribution shown in Fig. 2.23. It was rare to find two buds on the same node although a few incidences were found.

**Crowns**

A crown (Fig. 2.24) is formed on the woody stocks of *F. japonica* by the continual cycle of new stem growth in close proximity to the dead stems from previous years. Over time these can grow to become quite large in size (see Fig. 2.25), but since the crowns in this study were from the young periphery of the main stand they were relatively small in size.
Figure 2.23: Frequency distribution of lateral bud separations (n = 357).

Figure 2.26 shows some of the crowns extracted in this survey. Crowns 0–7 correspond to those shown in Fig. 2.5. The original location of crown 8 is unknown but is known to come from the vicinity of crown 7. Measurements taken of the crowns found in the subject area included approximate diameters, the number of shoots from previous years and the number of buds found (Tab. 2.10).

Figure 2.24: A crown showing the brown dead stems from previous years (A), green fresh stems (B), new shoots (C), ‘seals’ from fallen dead stems (D) and the stock (E).

Crown diameters were similar in size across the subject area with a range of 4–7 cm. Crowns can grow much larger than this in older stands, a feature that was evident in the main stand away from the periphery.

Old shoots are distinguishable from fresh stems by their brittle, dry texture and brown colouration (see Fig. 2.24). Fresh stems are pink/red or green with red flecks and new
Figure 2.25: An example of a large crown. A sense of the scale may be obtained by comparison of the crown with the standard house bricks seen in the lower left of the image. Picture: Lois Child.

Figure 2.26: Some of the crowns extracted from the survey site. Top (left to right): crown 1, crown 2 and crown 3. Bottom (left to right): crown 5, crown 7 and crown 8. The crowns in this study were relatively small due to being relatively young. Despite this, the elder crowns were the progenitors of extensive rhizome networks.
Table 2.10: Crown diameters, number of old shoots and number of dormant buds present.

<table>
<thead>
<tr>
<th>Crown</th>
<th>Diameter (cm)</th>
<th>Old shoots</th>
<th>Dormant buds</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>6</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>6</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>5.5</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>5</td>
<td>7</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>7</td>
<td>7</td>
<td>13</td>
<td>15</td>
</tr>
<tr>
<td>8</td>
<td>4.5</td>
<td>8</td>
<td>6</td>
</tr>
</tbody>
</table>

Shoots are softer and paler in colour. The number of old stems on each crown was counted including both those still attached to the crown and the scars (known as ‘seals’ [28]) left by those stems that had fallen previously. Crowns exhibited between 5 and 13 old stems with the most stems being found on crown 7 (one of the youngest). Figure 2.27 shows the frequency distribution for the nearest-neighbour stem separations, including both new stems and old dead stems as well as the seals.

![Histogram](image)

Figure 2.27: Frequency distribution of nearest-neighbouring stems on the crowns. These include both living and dead stems as well as the seals from older stems that were no longer present.

Figure 2.28 shows dormant buds on one of the crowns. When activated, these form new shoots such as those in Fig. 2.24 (C). Numbers ranged from 0–15 buds, with crown 7 exhibiting the most. There were no visible buds at all on crown 1.
2.3 Survey 2

The second survey was carried out in two parts, on the 19th November 2004 and the 27th April 2005. The main aims of this survey were to investigate rhizome growth rates and to obtain crown density data. Further nearest-neighbour crown separations were also obtained. This work was carried out with the assistance of Dr. Lois Child of the Centre for Environmental Studies at Loughborough University, Dr. John Ward of the Mathematical Sciences Department at Loughborough University and Dr. Markus Owen of the School of Mathematical Sciences at the University of Nottingham.

2.3.1 The Site

<table>
<thead>
<tr>
<th>General Site Information</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>O.S. National Grid Reference</td>
<td>SK470183</td>
</tr>
<tr>
<td>Location</td>
<td>Shepshed, Leicestershire, UK</td>
</tr>
<tr>
<td>Longitude</td>
<td>1:18:17W (−1.3047)</td>
</tr>
<tr>
<td>Latitude</td>
<td>52:45:38N (52.7604)</td>
</tr>
<tr>
<td>Altitude</td>
<td>Approx. 107 m above sea-level</td>
</tr>
<tr>
<td>Habitat Type</td>
<td>Road verge</td>
</tr>
<tr>
<td>Approx. Stand Area</td>
<td>56 m²</td>
</tr>
</tbody>
</table>

Table 2.11: General site information for the second survey

Table 2.11 details some general information about the second survey site. The site was on a roadside verge on the A512 through Shepshed (Leicestershire), directly opposite Brick
Kiln Lane. The stand itself was approximately 56 m² in area (see Section 2.3.2) and situated on a road verge, a few metres back from the pavement (Fig. 2.29).

![Image of the subject stand](image)

**Figure 2.29:** The subject stand for the second survey as viewed from the roadside.

The main stand consisted of a dense thicket of stems, both old and fresh, and many clearly defined crowns were present. The first part of this survey was carried out in November, meaning that most of the leaves had fallen and the plant was preparing for its overwintering state. However, a small mown area at the front of the stand exhibited some new shoot growth (see Fig. 2.30) which was possibly a direct result of the previous mowing releasing the buds from the restrictions of apical dominance.

### 2.3.2 Methods

This survey was conducted in two parts. The first involved the extraction of samples of new growth at the end of a growth season. The second part involved returning to the site soon after the beginning of the following growth season to investigate whether rhizome extension was a continuous process throughout the growth season or whether it occurred later following the mobilisation of stored nutrients and generation of new shoots early in the growth cycle. The density of the crowns in the stand was also measured at this time.

A small section at the front of the stand showed evidence of recent mowing which had clearly stimulated the development of new growth in that area (see Fig. 2.30), despite the main stand having already reached its overwintering state. The area designated for investigation of new rhizome growth was therefore chosen to be as far from the mown area as possible so as to negate any influence of the applied management. Figure 2.31 shows a sketch map of the subject site, marking the area of the stand that was unearthed.

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Figure 2.30: An area at the front of the stand showed evidence of recent mowing. New shoots could be seen still growing, whereas the main stand had no surviving new shoots. This illustrates how such management techniques as mowing can actually encourage plant growth.

Figure 2.31: A sketch map of the second survey site. The sample area marked was unearthed in order to extract samples of new rhizome growth.
Samples of new rhizome growth were identifiable by their white fleshy appearance (Fig. 2.32) as opposed to the hard, brown, woody-textured older rhizomes (see [18]). These were extracted in November 2004 at the end of the plant’s growth season and taken back to the lab for measurement. Evidence of the plant having reached its overwintering state consisted of the stems having turned brown, dry and brittle with very few leaves left attached.

![Figure 2.32: New rhizome growth was clearly identifiable by its white, fleshy appearance.](image)

In April 2005 the site was revisited in order to investigate rhizome growth early in the growth season and to obtain some data on crown density. The area of the stand is taken to be the area of the convex hull enveloping the stand’s constituent crowns (an ‘elastic band’ stretched around the stand). This was deemed to be the measure of area most readily comparable with simulation output. The number of crowns lying within this area were counted and the nearest-neighbour crown separations were also measured where possible.

### 2.3.3 Results

Identification of new growth was relatively easy, although some of the samples had begun to develop their darker overwintering state behind the fresh, white growth. However, it was found that even these darker parts still had a similar soft and fleshy texture to the white segments; they had not yet developed a tough, woody exterior in preparation for the winter. Table 2.12 details some of the data associated with the new growth.

The mean observed segment length of the new growth was 17.37 cm. Since this figure was obtained at the end of the growth season it is reasonable to take it as the mean rhizome extension per year. It is thus taken to be the step-length for a year in the correlated random walk model discussed in Chapter 3. It is noted, however, that the segment lengths were
<table>
<thead>
<tr>
<th>Number of sample segments</th>
<th>17</th>
</tr>
</thead>
<tbody>
<tr>
<td>Segment length mean</td>
<td>17.37 cm</td>
</tr>
<tr>
<td>Segment length std. dev.</td>
<td>9.22 cm</td>
</tr>
<tr>
<td>Segment diameter mean</td>
<td>0.34 cm</td>
</tr>
<tr>
<td>Segment diameter std. dev.</td>
<td>0.1 cm</td>
</tr>
<tr>
<td>Number of internode lengths</td>
<td>140</td>
</tr>
<tr>
<td>Internode length mean</td>
<td>1.74 cm</td>
</tr>
<tr>
<td>Internode length std. dev.</td>
<td>0.95 cm</td>
</tr>
</tbody>
</table>

Table 2.12: New rhizome growth sample data from the Shepshed site.

highly variable with a standard deviation of 9.22 cm. This motivates a possible modification to the model regarding variable step-lengths (see Section 3.6).

A mean segment diameter of 0.34 cm with a standard deviation of 0.1 cm illustrates how thin the new growth was. This supports the notion discussed in Section 2.2.3 that younger rhizomes thicken up with age.

None of the observed new growth exhibited any lateral buds or branching, suggesting that the formation of lateral buds and their subsequent generation of new branches are events that occur later in the rhizome's development. Many of the samples, however, did show evidence of node formation (Fig. 2.33).

![Figure 2.33: Evidence of node formation on new rhizome growth. Arrows show the location of nodes. The fresh sample on the left is shown *in situ* whilst the sample on the right has been allowed to dry out for a few weeks (hence its darker colour).](image)

The internode lengths obtained in this survey (Fig. 2.34) were compared with the equivalent data from the first survey (see Section 2.2.3). A $\chi^2$ test yields $\chi^2 = 17.656$ with 12 degrees of freedom (with all internodes over 6 cm in length grouped into a '> 6' interval to
satisfy the assumption of the $\chi^2$ test that each interval should have at least 5 members). It may therefore be stated with 87.35% confidence that the difference between the distributions from both surveys is not statistically significant. Since the data from this survey were obtained from new rhizome growth and those from survey 1 were from older rhizomes, this result suggests that once the nodes are formed on the new rhizomes there is no subsequent extension of the internodes over time. Thus, all longitudinal extension occurs at the apex of a rhizome and there is no elongation of rhizome segments behind the apex.

![Internode Length Distribution](image)

Figure 2.34: Frequency distribution of internode lengths obtained in survey 2.

A second visit to the site focused on the investigation of the density of crowns within the stand. For this, the area of the stand was defined as described in Section 2.3.2. Additionally, the circumference of the stand was also defined as the circumference of the convex hull formed by the crown locations. The circumference was found to be approximately 36.17 m and the stand area was approximately 55.74 m$^2$. In total, 79 individual crowns were identified within the stand, with 19 of these making up the convex hull of the stand. This gives a crown density of 1.4173 crowns per m$^2$ including perimeter crowns, or 1.0764 crowns per m$^2$ using internal crowns only. Hereafter the stand area calculated excluding the perimeter crowns is referred to as the ‘internal crown density’ and is used in Chapter 3 for model validation.

### 2.4 Discussion

The main aim of this fieldwork was to investigate the morphology and physiology of a rhizome network. This involved two surveys being undertaken, the extraction and measurement of various different features of a rhizome network and a number of surface measurements being taken. Morphological properties of the structure were easily obtained by direct observation
but understanding the physiology of the rhizome network was somewhat more problematic. Little is known about how the rhizomes in *F. japonica* develop and so some conclusions are drawn below based on available evidence and observations.

In the first survey, all of the rhizomes extracted were from no deeper than 50 cm below the soil surface with none found to extend from this level down, yet it is well known that rhizomes can grow to 2 m deep [18] and possibly even deeper. It is not known whether any rhizomes from the main stand extended any deeper than 50 cm into the subject area. This tendency for the observed rhizome growth to remain fairly shallow in the periphery may be due to a number reasons. Firstly, the type of substrate at greater depths may have made it difficult or more costly for deeper growth. There exist many anecdotal and published accounts of rhizomes behaving differently according to their substrate and environment (see, for example, [4]). In other sites the water-table may have presented a lower depth limit, but this was not a factor here since the slope was clearly above the water-table at its base. Another possibility is that since the subject area was on the periphery of a large stand, the rhizomes were serving a pioneering role by generally growing horizontally to colonise new ground. This is a typical feature of the plant in Japan, with long rhizomes being found relatively close to the surface [4]. It may therefore be the case that rhizomes initially serve a pioneering role by growing horizontally with later new rhizomes growing down deeper and fulfilling more of a storage and stabilisation role as crowns become more established and the availability of physical space becomes an issue. Further investigation of rhizome growth in both newly colonised and more established areas is required to confirm this or otherwise.

Rather than having tapered tips as expected, rhizomes were seen to exhibit blunt tips in general and no evidence of recent growth was found on such segments. They were also observed to be extremely tortuous in some cases, regardless of their diameter (as seen in Fig. 13). Additionally, rhizomes often had inconsistent diameters along the same segment, some of which were actually greater towards the tip than at the older base. This may have been due to the proximity and productivity of nearby stems and crowns. This suggests that the rhizomes might develop as follows:

1. New rhizomes develop in their first year as thin pioneering tendrils either from a crown or branching off of an existing segment. These extend for a time, negotiating the various obstacles they may encounter and forming nodes. No branching was observed on the new growth.

2. They then enter their overwintering state at the end of the growth season, forming the characteristic hard, woody-textured exterior and ceasing further longitudinal extension.

3. In subsequent growth seasons lateral buds are formed and new aerial shoots or rhi-
zome branches develop from these. As these shoots develop, perhaps forming crowns, nutrients are translocated to the rhizomes for storage and the older rhizomes begin to expand radially, increasing in girth rather than length to increase storage capacity, thus forming the observed blunt tips.

This is further supported by the observation in Section 2.3.3 that internodes do not seem to exhibit any further growth once they are formed.

It was found that there may be a relationship between the age, diameter and number of concentric rings exhibited in rhizome cross-sections. The strongest relationship was found between the diameter and the number of rings, a possible reason for which might be that the formation of the rings is dependent on the diameter of a segment rather than the age. If the diameter of a segment is directly related to the productivity of nearby crowns and stems, then it may be that it is this productivity rather than age of the rhizome that is the driving factor behind ring generation. If this is the case then the number of rings could not be used to estimate a rhizome's age in a similar way the annular rings in arboreal trees. Further investigation is required before any conclusions may be drawn.

Overall, the fieldwork was extremely successful in terms of elucidating a variety of different aspects of the morphology and physiology of rhizome networks in *F. japonica*. A large amount of previously unknown data was obtained and used directly in the modelling process (see Chapter 3) for both parameterisation and validation of the model. Many questions were answered and many new ones presented. As well as the data used directly in the modelling process, the results have also allowed an insight into many previously unknown aspects of the rhizome network's development. In particular, a good idea of the rate and manner in which rhizomes grow has been acquired including branching occurring some time after the new rhizome growth, branching occurring at lateral buds behind the apex rather than at the apex itself, and the lack of internode extension over time.

There is a large scope for extending this fieldwork further. The areas sampled in both surveys were reasonably representative of a typical habitat favoured by *F. japonica* that of a roadside verge/woodland. However, this only represents samples from a single habitat type. There are many different environments in which *F. japonica* may be found and it is reasonable to assume that its behaviour might be different in each. As well as the habitat type, environmental conditions such as pH values, availability of water, soil stability, water-tables, mineral content, altitude, sources of light and competition vary considerably from site to site and all play a significant part in the performance of the plant. It would be interesting to see how the data collected in these surveys compares with variations in any of these factors. Also, due to time constraints a lot of work that could otherwise have been done had to be foregone. It would have been extremely useful to see how data from the
centre of the established main stand in survey 1 compared with that from the periphery. It is expected that much larger crowns and rhizomes that extend much deeper would have been found here. However, such an investigation would have required a different method of extraction due to the lack of drainage. The main advantage of the pressure-washer method was that it allowed the network to be unearthed intact and caused only minimal damage to the rhizomes themselves. Deeper extraction would necessitate a more efficient method of bulk soil removal such as manual or mechanical digging, both of which would be far more damaging to the rhizomes.
Chapter 3

A Correlated Random Walk Model

All the evidence shows that God was actually quite a gambler, and the universe is a great casino, where dice are thrown, and roulette wheels spin on every occasion. Over a large number of bets, the odds even out and we can make predictions; that's why casino owners are so rich. But over a very small number of rolls of the dice, the uncertainty principle is very important.

*Stephen Hawking*

3.1 Introduction

Given the invasive nature of Japanese knotweed here in the UK, it is no wonder that it has come to the attention of many different councils, organisations, property developers, businesses and private landowners alike. Each of these parties has its own reasons for interest in the plant: damage to property, the threat to biodiversity, its effect on land prices, the cost and time associated with its removal etc. There is, therefore, a common desire to at least control, if not eradicate, the plant and its relentless spread. To this end, a number of different management strategies have been applied, each having its own merits, effectiveness, suitability, speed, risks, longevity and costs. It is thus extremely important to use the right strategy in the right circumstances. With this in mind, a tool that could test the impact and efficiency of these techniques both quickly and cheaply would be extremely useful indeed. Such a tool would also be useful in the prioritisation of infested sites for treatment and the promotion of the problem, for example by illustrating to landowners and councils how a stand might spread if left to grow untreated. As a first step towards building up more complex models, a correlated random walk model for the development of an unmanaged rhizome network for *F. japonica* in the UK is constructed. This model uses a great deal of the field data discussed in Chapter 2 in its parameterisation and validation. In this chapter,
the model itself is discussed, some results of simulations are presented and parameter surveys of unknown model parameters are carried out (also presented in [54]). Finally, a practical application of the model is demonstrated via the use of simulation results and costing data to predict future disposal costs of a problem stand of *F. japonica* in Cornwall, UK (also presented in [53]).

### 3.2 Model Overview

In this section a brief overview of the model is presented. A major component of the model is the use of a 3D correlated random walk (CRW) model to describe the growth of the rhizomes themselves. Random walks are discrete-time stochastic processes consisting of a sequence of discrete steps in random directions at each time-step. For simple random walks, the selected direction at any given time-step is independent of any previous choices of direction. In contrast, a correlated random walk changes direction in subsequent time-steps randomly, but with bounded range dependent on the previous direction of travel (Fig. 3.1). Such an approach has been used to model butterfly [42] and amoeboid movement [31] as well as a number of other species of animal. Cam (see [13]) was the first to apply this type of model to the vegetative spread of clonal plants. He constructed a CRW model in 2D for the development of a rhizome network in the old-field perennial *Solidago altissima* (goldenrod), the parameter values of which were obtained directly from field studies. Here a similar approach is taken with the construction of a 3D CRW model with a number of additional features for the development of *F. japonica* rhizome networks.

![Figure 3.1](image)

**Figure 3.1** An example of one step in a correlated random walk. Here a is the previous growth vector, b is a potential choice of direction for this time-step and δ is the maximum deviation. The dashed lines represent the maximum possible change of direction in this plane for this step and the continuation of the previous growth vector.

Rhizomes can grow up to 2 m deep [18], meaning that their vertical growth can play as
important a part in the development of the network as the horizontal growth, for example, in overcoming obstacles in the plant's path such as walls or roads that might typically affect growth patterns at this scale. Additionally, in agreement with the observations of Adachi et al. [2], the data from this study shows no crowns developing below 30 cm from the surface. It is thus necessary that the model can accommodate this key feature of the rhizome's development and this assumption is used to impose a limit on the depth at which crowns may form. Furthermore, the field data features significantly in the model and in many cases these data by their very nature implicate the use of a three dimensional model. For example, the segment lengths are purely the length of a segment, not the distance in the x-y plane that the segment tip was separated from its base. This is also true of the branching angles which were measured relative to their parent segment, not a fixed reference point. The use of three dimensions allows us to use these data, thereby making the model closer to the biology. Other important properties of the plant that should also be included in the model are the erratic changes in direction that rhizomes make, the formation of crowns to facilitate the extension of the network, typical branching angles and segment lengths, and a range of other empirically determined physiological parameters.

Figure 3.2 illustrates the basic model in a top-down view. As an initial condition, a single shoot or crown is set at the origin. Biologically this may have been the result of the regeneration of a scattered fragment of rhizome, perhaps by human-influenced disturbance such as the transport of contaminated soil or the incorrect application of management techniques such as mowing or flailing. This is a common way for the plant to be spread into new habitats. This single crown develops a few rhizomes which emanate from it at directions randomly chosen from a uniform distribution but limited to $z \leq 0$ in a Cartesian coordinate frame. At each time-step these rhizomes grow according to the CRW process. Once they have grown long enough, branching may occur or new crowns may form. When a new crown forms, it then generates new rhizome segments in the same way as the initial crown. Branching and crown formation events are controlled by random draws from probability distributions and look-up tables created from the field data. Eventually, a set of crowns that are interlinked by rhizome networks is formed. The model is discussed in more detail in Section 3.3, in which simulations of the model are also described.

### 3.3 Simulation of the Correlated Random Walk Model

In this section, a simulation of the CRW model is detailed. The simulation focuses on the development of a stand of *F. japonica* from a single pioneering rhizome fragment to a full system of mature crowns interconnected by a growing and branching rhizome network. It
Figure 3.2: A simple illustration of the CRW model (top-down view). Left to right: i) Initial conditions consist of a single crown which emits rhizome segments in random directions. ii) These rhizome segment then extend via the correlated random walk process. iii) Once a segment is long enough, branching occurs. iv) New crowns are formed according to probability distributions gleaned from the field data (subject to certain conditions). These then send out new rhizome segments in the same way as the initial crown. In this way a set of crowns interlinked by networks of rhizome segments is formed.

consists of a series of rules and events that are carried out at each time-step according to various probability distributions and parameter values drawn from the field data (see Chapter 2). The simulation was coded in the software package Matlab and works as follows:

1. **Initialise.** Anything stored in memory is cleared. The ‘state’ for the random number generator is randomised by generating its seed from the internal clock¹.

2. **Begin set of trials.** Trials for the current set of parameter values are initiated. The number of trials to run, \( R \), is set and a store for information about failed runs is created.

3. **Begin trial.** Simulation timer is started and trial begun. If this is not the first trial in the set, relevant stored data is cleared.

4. **Set parameters and variables.** Parameters and variables are set including:
   - Location of the initial crown.
   - A store for the number of crowns present, initialised to 1 in all simulations.

¹Using the ‘state’ method in Matlab’s ‘rand’ command produces double precision values and can theoretically generate over \( 2^{1492} \) values before repeating itself.
• The number of rhizomes each crown will emit, \(r\).
• The number of time-steps to run each trial for, \(n\).
• The maximum branching order (see Section 2.2.3 for an explanation of the ordering used) of a rhizome, \(\gamma\). The field data from Cornwall yielded no examples of a branching order traced from a parent crown of greater than 3.
• The rhizome extension in metres per time-step, \(l\). This parameter was taken from the mean length of new growth found at the Shepshed site (see Section 2.2.3).
• The nearest neighbouring crown separations from both survey sites.
• The mean trans-network separations of linked crowns, \(d\). This is taken to be the mean of equivalent measurements from the Cornwall survey site data. In the simulation it represents a qualifying condition for which a segment could develop a new crown once \(d\) is exceeded.
• The probability that a crown will form at the current segment tip location given that all other qualifying conditions have been met, \(c\).
• The maximum depth at which crowns may form, \(h_c\). In the field this was not seen to exceed 30 cm which is in agreement with the findings of Adachi et al. [2].
• The maximum deviation in degrees from the previous direction of growth, \(\delta\).
• The minimum and maximum depths at which rhizomes may grow, \(h_{\text{min}}, h_{\text{max}}\). These depth constraints are taken to be zero-flux.
• The segment lengths measured from Cornwall site samples. These are used to create a lookup table from which a branching trigger length is randomly assigned to each segment as it is created. This method facilitates the inclusion of further data as it becomes available without the need to alter the simulation.
• The probability of the rhizome not growing at any given time-step, \(p_p\).
• The probability that a rhizome ceases growing permanently (‘dies’), \(p_d\).
• The branching angle data from the Cornwall site. A lookup table is created from which new daughter rhizomes are randomly assigned a branching angle.

Table 3.1 details the parameter values used in the standard simulations, some of which were extracted from the field data.

5 Initial setup A store of the time-step at which crowns are formed is created for use in output movie-making. Stores of segment tip locations and segment histories are created. A store of active rhizomes is created.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Std. Values</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhizome extension per year</td>
<td>( l )</td>
<td>0.174 m</td>
<td>Data from fieldwork</td>
</tr>
<tr>
<td>Branching angles</td>
<td>n/a</td>
<td>6–90°</td>
<td>Data from fieldwork</td>
</tr>
<tr>
<td>Nearest-neighbour crown separations</td>
<td>n/a</td>
<td>0.17–1.44 cm</td>
<td>Data from fieldwork †</td>
</tr>
<tr>
<td>Trans-network crown trigger length</td>
<td>( d )</td>
<td>0.8611 cm</td>
<td>Data from fieldwork</td>
</tr>
<tr>
<td>Primary segments from new crowns</td>
<td>( r )</td>
<td>2</td>
<td>Data from fieldwork</td>
</tr>
<tr>
<td>Probability of forming a crown</td>
<td>( c )</td>
<td>0.0145</td>
<td>Estimate</td>
</tr>
<tr>
<td>Maximum branching order</td>
<td>( \gamma )</td>
<td>3</td>
<td>Data from fieldwork</td>
</tr>
<tr>
<td>Maximum crown formation depth</td>
<td>( h_c )</td>
<td>-30 cm</td>
<td>Data from fieldwork</td>
</tr>
<tr>
<td>Maximum deviation of growing tips</td>
<td>( \delta )</td>
<td>20°</td>
<td>Estimate ‡</td>
</tr>
<tr>
<td>Min depth limit of rhizome growth</td>
<td>( h_{\text{min}} )</td>
<td>0 m</td>
<td>See [18]</td>
</tr>
<tr>
<td>Max depth limit of rhizome growth</td>
<td>( h_{\text{max}} )</td>
<td>-2 m</td>
<td>See [18]</td>
</tr>
<tr>
<td>Prob of no growth this time-step</td>
<td>( p_{p} )</td>
<td>0.01</td>
<td>Estimate</td>
</tr>
<tr>
<td>Branching trigger lengths</td>
<td>n/a</td>
<td>0.6–81.1 cm</td>
<td>Data from fieldwork †</td>
</tr>
<tr>
<td>Prob of segment dying</td>
<td>( p_{d} )</td>
<td>0.0083</td>
<td>Taken to be ( l/7 ) for expected length of 7 m</td>
</tr>
</tbody>
</table>

Table 3.1 Standard simulation parameters Standard simulations were run for 200 time-steps (1 time-step = 4 months) Estimated parameters were chosen such that, on average, a crown density comparable to that observed in the field was obtained †Chosen in the simulation via the use of look-up tables ‡Although the sample shown in Figure 1.3 exhibits extremely tortuous growth, in general rhizomes were much straighter.
Starting from the location of the initial crown, a direction for each of the initial rhizomes to grow in is chosen randomly from the $z \leq 0$ hemisphere ($z = 0$ being the surface of the substrate). These choices are then checked to make sure that they do not clash with each other and lie within the boundaries $h_{\text{min}}$ and $h_{\text{max}}$. If either of these conditions fails, the direction selection process is repeated until both are passed.

The number of rhizomes in existence is stored and the initial crown is assigned a radius around it in which no new crowns may form. This is achieved by randomly selecting a radius from the distribution of nearest neighboring crowns. This area surrounding the crown in which new crown generation can not occur represents the intraspecific competition from ground litter, leaf-shading and physical space restrictions that would prevent any new crowns from forming in the field, thereby recreating a simple crowding response.

Each new rhizome is assigned a branching trigger length. These are randomly chosen from the lookup table of segment lengths from the Cornwall site. Once this trigger length is reached, assuming the segment is not at its maximum branching order, the segment will produce a bud. In the following growth season, this bud will become a new daughter rhizome segment. This mechanism represents a phenomenological account for apical dominance and hormone-controlled branching events.

6 **Advance time** Stores of crown densities and ‘buds’ (future daughter rhizomes, initially empty) are created. Time is advanced one time-step. Stores of new daughter rhizome information and rhizome growth from new crowns are cleared/created.

7 **Develop buds** Here, a ‘bud’ is a location at which a new daughter rhizome will form after the set time-delay (one growth season) rather than the biological bud. Buds only develop on active (not dead) rhizomes. The order in which the active rhizomes are checked for bud formation is randomised at every time-step. The length of each segment is checked against its predetermined branching trigger length (see step 5). If the trigger length has been attained the segment becomes inactive and produces a continuation segment (continues growing in approximately the same direction as its ‘parent’) and a bud (see step 5) at its tip. However, if the segment is already at its maximum branching order then it can not produce any progeny and thus simply becomes inactive. All relevant stores are updated.

8 **Develop new crowns** The order in which the active rhizomes are checked for crown formation is randomised at every time-step to prevent any bias in the arrangement of crowns and rhizome development. Crowns form at the tip of rhizome segments and a
number of conditions must be met before a new crown can form. Firstly, the tip must be in a location viable for new crown generation (see 5). Secondly, the trans-network distance of the tip from its parent crown must be greater than \( d \) (see Table 3.1 and step 4). Finally, the tip must be within the empirically-obtained valid depth limit for crown generation, \( h_e \) (see step 4). For each segment, if these conditions are passed there is a chance that a new crown will form. If a new crown does form, a new intraspecific competition radius is created for it and its parent segment is made inactive. Crowns are known to produce lateral creeping rhizomes within their first year [6], so the new crown then generates its own rhizomes in the same way as the initial crown and all relevant stores are updated.

9 Branching. If any buds exist, they are checked to see whether they have reached the required age for activation. Observations from survey 2 (see Section 2.3.3) yielded no incidences of branching in the new rhizome growth. Therefore, for a segment to branch it must be old enough to have gone through at least one overwintering state to develop lateral buds. Thus, the activation of simulated buds occurs one full year (3 time-steps, see step 10) from the time of their creation. In a random order each active bud is turned into a new daughter rhizome. These are treated the same as any other rhizome except that the angle at which they branch from their parent segment is randomly chosen from the branching angle lookup table created from the field data. All relevant stores are updated and the new rhizomes are assigned a generation number equal to that of their parent segment plus one.

10 Correlated random walk. Each active rhizome segment undergoes one step of a correlated random walk (see Figure 3.1). This excludes the new daughter segments and primary rhizomes from new crowns which have already had their directions assigned for this time-step. It also excludes those segments that do not grow for this time-step only, randomly determined by failing a test against \( P_p \). The extension per unit time of rhizomes is taken to be the mean of the new growth data (see Section 2.3) divided by 3, meaning that one time-step is 4 months (1/3 year). This meant that extension per unit time was short enough to provide a reasonable scope for rapid change of direction whilst retaining a convenient unit of time. The change in direction from the previous time-step is randomly chosen from a uniform distribution such that the magnitude of the angle between the previous growth direction and the proposed one is in the range 0-\( \delta^\circ \). Validity of the newly chosen directions is checked, failures are re-chosen and path histories are updated.

11 Segment death. In addition to segments dying when they have reached their branch-
ing trigger length at the maximum prescribed branching order from their parent crown, there is also a small chance, \( p_d \), of each rhizome segment expiring irrespective of its branching order. If all segments are dead, the current simulation trial terminates here, details of the trial are recorded and the simulation returns to step 3 to begin the next trial.

12 Calculate crown densities The area of the stand, \( A \), is defined to be the area of the convex hull (the shape made by an ‘elastic band’ stretched around the stand) defined by the stand’s constituent crowns. If \( A < 1 \text{ m}^2 \), the area is taken to be 1 m\(^2\) to avoid unrealistically large crown densities being calculated and, generally, only those time-steps for which \( A > 1 \text{ m}^2 \) are included in the analyses. Three different crown densities are calculated: The first is the number of crowns within a square metre centred on the origin (the initial crown). The second gives the number of crowns including those on the boundary of the convex hull per square metre. The third excludes the crowns that make up the convex hull. For the purpose of analyses, the third type, referred to as the ‘internal crown density’, is focused upon. For \( A \) to exist, the stand must consist of at least 3 distinct crowns, and thus time-periods in which there are less than 3 crowns in the stand are generally ignored in the analysis of results. Simulation output data is then stored and steps 6–12 are repeated for the remaining steps in the trial. If this is the final step in a particular trial, the next trial is started (step 3).

13 Statistical analysis If this is the final trial in the set, various statistics about the trials are calculated and stored. If there are multiple parameter values to be investigated, the relevant parameter is changed and the process repeated from step 2.

The time taken for simulations to run is highly dependent on many factors. Most influential are the parameter values themselves since these directly influence the number of calculations to be performed by the processor in a variety of ways. Pseudo-random effects resulting from the stochastic nature of the simulation, such as the generation of crowns in viable zones, can also make the simulation more (or less) processor-intensive. Obviously, simulation times are also highly dependent on hardware specification. The available computing resources and time available did impose some restrictions on the parameter sets feasible for investigation (detailed in Section 3.4.3), but generally this was not an issue for the scope of this work. For simulations run under the standard parameter set, the time taken to complete the 200 time-steps was, on average, around 5 hours\(^2\). However, the longest simulations

\(^2\)Simulations were generally run on an Apple Mac dual 533 MHz PowerPC G4 with 768 MB SDRAM and running OS X.
undertaken in this study was a set of three that lasted an average of 65.7 hours each for 
c = 0.29, due to the large number of crowns generated

3.4 Results

In this section the results of simulations of the CRW model are discussed. Results obtained 
from simulations of the model run under the standard parameter values are presented, fol­
lowed by extensive parameter surveys that were carried out in order to investigate the effects 
of the unknown parameters (those that were not directly acquirable from the field data) on 
the model output. The sensitivity of the model on the known parameters is also tested. 
Since these represent physical properties of the plant, this may have some implications for 
management applications.

Analysis of the simulation output is generally presented with particular reference to crown 
density and the rate of area expansion. These represent two easily-measured field properties 
and thus serve as convenient characteristics with which to compare standard simulations, 
the results of parameter surveys and field observations for model validation purposes.

The stochastic nature of the simulation means that no two simulations will produce 
identical output. Figure 3.3 shows a top-down view of the location of crowns in a simulated 
rhizome network in which it is clear that there is no evident order in their spatial location. 
Other simulations run under the same parameter values can produce results varying from no 
ew new crowns being produced (either through entire stand death or by all rhizomes growing 
below the required depth limit for new crown growth) to many more than shown in Figure 
3.3. This variability must be accounted for in any analysis of the model output. Therefore, 
multiple trials were carried out for all parameter settings investigated in order to obtain the 
mean and standard deviation of the model’s behaviour.

3.4.1 Standard Parameters

Figures 3.4 and 3.5 show a typical output of the simulation run under the standard parameter 
set. Note the lack of order in the spatial locations of the crowns and the highly variable 
separations between them. Also note the tendency for the rhizomes to spread some distance 
away from the main body of the aerial stems. Standard simulations were run for 200 time-
steps (about 67 years) unless otherwise stated. The standard parameter set used is detailed 
in Section 3.3 and summarised in Table 3.1.

Figure 3.6 shows the mean crown density (left) and mean area evolution (right) with time 
for a typical standard simulation of the model. It can be seen that the crown density tends
to settle at around 1 crown per square metre from around $t = 120$ onwards. This conforms with the density observed in the field of 1.08 crowns per square metre (see Section 2.3.3), one of the benchmarks used for model validation.

Fitting a least-squares polynomial to the mean area with time yields a very strong correlation to a quadratic expansion of area in time ($R^2 = 0.999$). Here, the area of the stand is taken to be the area of the convex hull formed around the simulated stand’s constituent crowns. This quadratic expansion in area, $A$, occurs in all simulations, the important consequence being that in large time

$$A \approx \alpha t^2$$  \hspace{1cm} (3.1)

for some constant $\alpha$. For the standard parameter set, 14 trials yielded a value of $\alpha = 0.0035$. This constant indicates how fast a stand will grow and, consequently, it is a useful parameter for characterising the effects of the unknown parameters in the parameter surveys (Section 3.4.2). Note that for the statistical analysis, only those trials of the simulation that did not fail (whole stand dies) are included so as not to skew the statistics. Indeed, the fieldwork focused only on thriving stands. For 19 trials run under the standard parameter values, no incidences of the entire stand dying were observed.

The prediction of the model that stand area should grow quadratically in time presents an additional benchmark for use in model validation. However, relevant data with which to test this prediction against has not yet been obtainable. This is, in part, due to the fact that the model is based on the development of a rhizome network in a homogeneous environment, using data from stands located in the UK from a single habitat type. Existing data that

Figure 3.3: The spatial distribution of crowns generated by a typical simulation of the CRW model run over 155 time-steps. Here, 61 crowns have been generated. The inherent stochasticity of the model is clear to see with little order evident in the location of generated crowns. The dashed line defines the convex hull used to determine the area of the simulated stand.
Figure 3.4: A 2D top-down view of a typical output of the simulation at 200 time-steps ($\approx 67$ years). Crown locations are marked with a green dots and the rhizomes are shown in brown.
Figure 3.5: A 3D view of a typical output of the simulation at 200 time-steps (≈ 67 years). Crown locations are marked with a green dots and the rhizomes are shown in brown.
Figure 3.6: Mean crown density (left, 18 trials per data point) and mean area evolution (right, 14 trials per data point) (solid lines) and ±1 standard deviation (dotted) against time for simulations of the model run under the standard parameter values (Tab. 3.1). The dashed curve in the right figure indicates the best least-squares fit to a quadratic function.

would otherwise be of use here is often drawn from stands subject to external influences such as management (both inhibiting and encouraging growth in different circumstances) or the influence of watercourses which can strongly assist the plant’s spread. The author is aware of two separate field experiments that are currently underway that will yield results useful in confirming (or otherwise) this prediction, but these data will not be available for at least two years hence. Should field experiments also show quadratic growth in area, the model would be extremely useful in the assessment of disposal costs for infested sites. This is discussed further in Section 3.5.

### 3.4.2 Parameter Surveys

Simulation output can vary markedly according to the values assigned to the various governing parameters of the system. This is illustrated in Figure 3.7. It is clear to see how changing $\delta$ affects the behaviour of the system. For $\delta = 5^\circ$, rhizome segments are relatively straight and, as a result, have moved away from the initial crown much more quickly than for larger $\delta$. This means rhizome tips have reached areas viable for new crown generation much sooner and hence generated 12 crowns in total. For $\delta = 20^\circ$ (standard), rhizome segments are much more tortuous and exhibit large changes in their direction of growth, as seen in the field. Rhizomes have therefore moved away from the initial crown less quickly and so the tips have not reached as many areas valid for new crown generation and fewer are formed. This effect is accentuated even further for the biologically irrelevant case $\delta = 180^\circ$. Extremely tortuous
rhizomes have formed a dense cluster around the initial crown, meaning that no rhizome tips have yet managed to produce any new crowns.

Figure 3.7: An example of how changes in parameter values can affect model output. Here, the simulation is run for only 70 time-steps for clarity and $\delta$ is varied from $\delta = 5^\circ$ (left) to $\delta = 20^\circ$ (centre) to $\delta = 180^\circ$ (right). Note the large changes in behaviour between simulations run under the three different parameter values, particularly the number of crowns generated, the area covered by the rhizomes and how tortuous the rhizomes are.

Clearly the effect $\delta$ has on the model output is significant and this is only one of many parameters in the model. Accurate parameterisation of the model is therefore essential if realistic and valid results are to be obtained. The use of field-data in the model meant that appropriate values for the majority of the parameters were attainable. Only three parameter values remained unknown: $c$, $\delta$ and $p_p$ (see Tab. 3.1). With so few unknowns it was possible to carry out an extensive study on the effect of these parameters on the model output. The stand characteristics studied in the parameter surveys below are crown density and stand growth coefficient $\alpha$ (see equation (3.1)). Statistics were taken from those simulations that produced fully established stands. This was defined to be stands that had exhibited area expansion for at least 50 time-steps. Stands that had not exhibited area expansion for at least 50 time-steps were omitted from the statistics. For stands that completely died out the number of trials included in the statistics are noted in the text.

**Maximum Deviation, $\delta$**

Figure 3.8 shows the relationship between the maximum deviation (angle of maximum turn) allowed in the correlated random walk, $\delta$, and the mean crown density (left) and $\alpha$ (right).

For $0 \leq \delta \leq 40^\circ$ the predicted crown density remains almost constant at just over 1 crown per square metre. For $\delta > 40^\circ$ the general trend is monotonically increasing with greater variability exhibited for larger $\delta$. This is due to large $\delta$ resulting in a slower rate of
Figure 3.8: The effects of $\delta$ (in degrees) on mean crown density (left, 5–18 trials per data point) and growth parameter $\alpha$ (right, 3–14 trials per data point). Bars indicate $\pm 1$ standard deviation. Other parameters in the trials are as given in Tab. 3.1.

area expansion (see below) which means that rhizomes have a higher likelihood of ‘filling in the gaps’ with new crowns, leading to the observed higher crown density.

For $\delta \geq 10^\circ$ the area expansion curve is monotonically decreasing with increasing $\delta$ as expected. The relatively low value for $\alpha$ in the vicinity of the biologically unlikely case $\delta = 0^\circ$ is an artifact of the way the simulation works. The depth boundaries are zero-flux and if a segment exceeds the depth limit during its growth phase then it is adjusted such that its tip lies on the boundary. Therefore, since for $\delta = 0^\circ$ there is no change of direction from one time-step to the next, once a segment reaches either boundary it will continue to grow along that boundary. As the simulation progresses this means that many rhizome segments will have grown beneath the maximum depth required for crown generation with no chance of re-entering the viable zone, resulting in an artificially reduced mean value for $\alpha$.

The fastest growth in area is exhibited in the range of 5–40°, after which area expansion becomes almost negligible in the studied time-scale. This is due to the generation of highly tortuous rhizome segments, resulting in a restricted outward expansion and, hence, a reduced growth rate. It is therefore likely that an appropriate value for $\delta$ lies within the range of 5–40°, which is also supported by the predicted mean crown density above. In the absence of crown growth and rhizome death, the case in which $\delta = 180^\circ$ is equivalent to the rhizomes undertaking a simple random walk rather than a correlated one. However, it is noted that since growth is occurring, the $A \approx \alpha t^2$ behaviour is preserved in this case.

No stand deaths were observed for simulations run under all parameter values except $\delta = 70^\circ$ (1 out of 9 trials) and $\delta = 170^\circ$ (2 out of 46 trials).
Probability of a Crown Forming, \( c \)

Figure 3.9 shows the relationship between \( c \), the probability of a crown forming at the tip of a rhizome segment given that all of the other prerequisite conditions have been met, and the mean crown density (left) and \( \alpha \) (right).

Figure 3.9 The effects of \( c \) on mean crown density (left, 3–18 trials per data point) and growth parameter \( \alpha \) (right, 3–14 trials per data point) Bars indicate \( \pm 1 \) standard deviation Other parameters in the trials are as given in Tab 3.1.

The general trend exhibited by the mean crown density is monotonically increasing with \( c \) as expected. The crown density observed in the field of 1.08 crowns m\(^{-2}\) suggests that an appropriate value for \( c \) lies in the range 0.0029–0.0145.

The general shape of the area curve indicates that \( \alpha \) increases monotonically with \( c \) with the greatest change occurring between \( c = 0.005 \) to \( c = 0.05 \). For \( c > 0.05 \) the intraspecific competition conditions play a much greater role in limiting the rate of area expansion due to the higher incidence of crown generation. For small \( c \) the predicted mean value for \( \alpha \) is very small and will vanish as \( c \to 0 \). This is mainly due to the fact that the probability of a segment ‘dying’ (no further growth permanently), \( p_d \), becomes much larger than \( c \) and hence rhizome segments are far more likely to die before they have a chance to develop a new crown.

No stand deaths were observed for simulations run under all parameter values except \( c = 0.003625 \) (3 out of 100 trials), \( c = 0.0014 \) (2 out of 12 trials) and \( c = 0.0072 \) (1 out of 6 trials).
Probability of a Rhizome Remaining Stationary, \( p_p \)

Figure 3.10 shows the relationship between \( p_p \), the probability that a rhizome will not grow at any given time-step, and the mean crown density (left) and \( \alpha \) (right).

Figure 3.10  The effects of \( p_p \) on mean crown density (left, 7-18 trials per data point) and growth parameter \( \alpha \) (right, 6-14 trials per data point). Bars indicate ± 1 standard deviation. Other parameters in the trials are as given in Table 3.1.

The mean crown density predicted by the simulations is not significantly affected for \( p_p \in [0, 0.4] \) with predicted densities lying in the range 1-1.2 crowns m\(^{-2}\), but for \( p_p > 0.4 \) the general trend is monotonically increasing with \( p_p \). This is explained by the increase in time spent in viable areas due to the slower rate of extension caused by the increased incidence of rhizomes remaining stationary.

As expected, the rate of area expansion is greatest for \( p_p = 0 \), for which there is no retardation of extension, and zero for \( p_p = 1 \) since no growth will occur on any time scale. The growth rate of the stand decreases with increasing \( p_p \) since each rhizome is less likely to survive to form a crown due to random expiration (\( p_d \)) becoming an increasingly dominant factor. Indeed, no stand deaths were observed for simulations run under all parameter values except for \( p_p = 0.1 \) (1 out of 10 trials), \( p_p = 0.8 \) (2 out of 18 trials) and, most significantly, \( p_p = 0.9 \) (30 out of 177 trials).

### 3.4.3 Variation of Known Parameters

Whilst many of the parameter values required for the model were directly measurable from the field samples, it is still of interest to investigate the effects that varying these has on the model output in a similar fashion to the parameter surveys detailed in Section 3.4.2. Since
in many cases these represent physical properties of the plant, knowing their influence on the rhizome network's development might allow for management techniques that directly target particularly influential parameters. As a trivial example, increasing the chance of rhizome segments dying ($p_d$) would result in increased instances of the death of the entire simulated stand. One might therefore consider the application of herbicide to increase $p_d$ in the field and hence kill a stand.

Due to computing limitations, investigations into the effects of the known parameters were performed, although not as extensively as those discussed in Section 3.4.2. Preliminary work suggests the following results might be obtained upon further investigation:

**Probability of a segment dying, $p_d$**

Figure 3.11 shows the effects of $p_d$ on mean crown density and growth parameter $\alpha$. It was expected that both crown density and $\alpha$ would decrease monotonically with increasing $p_d$ due to the increased incidence of segment death retarding stand expansion (so that fewer areas viable for new crown generation are reached). However, after an initial small drop, the mean crown density seems to remain reasonably constant over the range investigated. In contrast, $\alpha$ does seem to be affected by $p_d$, showing an initial small increase (which may just be an artifact of the small sample size) to a maximum followed by a monotonic decrease thereafter for increasing $p_d$. Rates of entire stand death would be expected to increase with $p_d$, although statistics are unavailable at present.

![Figure 3.11](image)

Figure 3.11 The effects (2–18 trials per data point) of $p_d$ on mean crown density (left) and growth parameter $\alpha$ (right). Bars indicate ±1 standard deviation. Other parameters in the trials are as given in Tab. 3.1.
Number of rhizomes generated by new crowns, \( r \)

Figure 3.12 shows the effects of \( r \) on mean crown density and growth parameter \( \alpha \). No simulations were carried out for \( r > 3 \) since they rapidly became prohibitively processor-intensive for the available computing resources. However, for \( r = 1, 2, 3 \) the crown density and \( \alpha \) both seem to increase almost linearly with \( r \). It is expected that this will reach a limit for higher \( r \) due to the built-in intraspecific competition in the model.

![Figure 3.12](image)

Figure 3.12 The effects (3–30 trials per data point) of \( r \) on mean crown density (left) and growth parameter \( \alpha \) (right). Bars indicate ±1 standard deviation. Other parameters in the trials are as given in Tab 3.1.

Maximum branching order, \( \gamma \)

Variation of \( \gamma \) was also restricted by computing resources. For \( \gamma > 3 \) simulations were again too expensive in computation time. Also, \( \gamma = 1 \) causes almost immediate stand death in the simulation since the segments become inactive once they reach their first branching points and hence no new crowns are formed. Setting \( \gamma = 2 \) also causes a significant increase in entire stand death rates over the standard \( \gamma = 3 \), with 7 of 13 trials (≈ 54%) resulting in entire stand death before 200 time-steps. None of the simulations carried out for \( \gamma = 2 \) resulted in any stand development prior to 150 time-steps and hence the statistics are neglected here.

Maximum crown formation depth, \( h_c \)

Figure 3.13 shows the effects of \( h_c \) on mean crown density and growth parameter \( \alpha \). Decreasing \( h_c \) from \(-0.1\) to \(-0.7\) in deep results in a small rise in crown density, although it is relatively insignificant and may only be a result of the inherent stochasticity of the simulations. Further simulations may yield different results. However, \( \alpha \) does seem to exhibit
a generally increasing trend with deeper $h_c$. This is because allowing crown generation at greater depths means that fewer rhizomes escape the viable zone and, hence, more crowns are likely to be formed which results in faster stand expansion.

![Graphs showing the effects of $h_c$ on mean crown density and growth parameter $\alpha$.](image)

Figure 3.13 The effects (3-18 trials per data point) of $h_c$ on mean crown density (left) and growth parameter $\alpha$ (right). Bars indicate ±1 standard deviation. Other parameters in the trials are as given in Tab. 3.1

**Maximum depth limit of rhizome growth, $h_{\text{max}}$**

Figure 3.14 shows the effects of $h_{\text{max}}$ on mean crown density and growth parameter $\alpha$. For $h_{\text{max}} > h_c$, crown density is higher than normal since all rhizomes remain in a zone viable for crown generation (so long as another crown is not already present nearby), but for $h_{\text{max}} < h_c$ the crown density returns to the level of the standard simulations and remains largely unaffected by decreasing $h_{\text{max}}$ further. A gradual monotonic reduction in $\alpha$ is seen as $h_{\text{max}}$ becomes more negative. This is likely due to the increasing depth providing more and more space for the rhizomes to grow down below the viable zone. The deeper this is, the less likely deep rhizomes are to return to the viable zone and so the slower the stand will expand.

### 3.5 Using the Model for Evaluation of Disposal Costs: A Case Study

In delay there lies no plenty

*William Shakespeare*
Figure 3.14 The effects (3-18 trials per data point) of $h_{max}$ on mean crown density (left) and growth parameter $\alpha$ (right). Bars indicate $\pm 1$ standard deviation. Other parameters in the trials are as given in Tab 3.1.

One of the primary motivations for the development of the models contained in this report was so that they could be used as a tool to demonstrate to those parties concerned the potential economic costs of failing to apply management on sites where knotweed is present. Graphical illustration of how a stand might look in the future if left untreated is one way in which the models might achieve this (see, for example, Fig 4.6 in Section 4.3).

Another, perhaps more influential factor to be taken into consideration is the increase in financial cost of removal over time. Aside from the size of the stand itself, there are many factors affecting the exact cost at any given site including the distance the contaminated soil has to be transported, local variations in tipping charges, taxation, machinery hire and so on. Here, one specific site (for which data was available) is considered and the potential increase in the estimated cost of removal over time is illustrated using model predictions. Unless otherwise stated, all data/costs used in this study were provided by Cornwall County Council and constitute a part of a research bid. In general, the figures quoted are likely to be highly variable between specific sites.

For this case study, a stand of *F. japonica* near Penzance (Cornwall) is considered. Here, a stand of approximately 25 m$^2$ in area needs to be removed. In this case, ‘removal’ of a stand of *F. japonica* from a site means the excavation of contaminated soil and burial at a specialist disposal site. Estimation of the total cost is therefore made up of the following elements:

- Volume of contaminated soil to be removed. Rhizomes may grow to 2 m deep [18], but some sources report them being found as deep as 3 m. As a result, it may be necessary to excavate anything from 0.9-3 m deep. They can also grow between 3
and 7 m laterally from the visible edge of the above-ground stand. The volume of contaminated soil to be disposed of can therefore vary considerably. The subject stand is currently 5 m x 5 m (25 m²) in area, meaning that the area covered by the rhizomes could extend from 11 m x 11 m (121 m²) to 19 m x 19 m (361 m²). Coupling this with the possible depth range of 0.9–3 m yields a potential volume of contaminated soil of between 121 x 0.9 = 109 m³ and 361 x 3 = 1083 m³.

- **Mass** The mass of different substrates can vary greatly (e.g., clay is generally heavier than sandy soil). Knowledge of the mass of the soil is important for two reasons: i) the vehicle used to transport the material will be limited in the weight it can carry as well as the volume and ii) the cost of tipping will depend on the mass of the soil removed. For the Penzance site, a mass of 0.75 tonnes per cubic metre of soil is assumed. However, this is likely to be a very conservative estimate, perhaps for a load consisting mainly of rhizome and other plant material with little soil. Truitt [58] gives typical unit weights for various soils in both dry and saturated states. The mean of the dry (135 lb/cu ft) and saturated (145 lb/cu ft) unit weights for a well-graded mixture of gravel, sand, and clay is taken as a representative field unit weight. This gives an assumed unit weight of 140 lb/cu ft, or 2.242 tonnes per cubic metre.

- **Excavation** This cost covers the machinery hire, labour costs, and any other costs related to the extraction of the contaminated soil from the site. It is estimated that excavation will take 1–2 days at a cost of £300 per day.

- **Transportation** At present there are relatively few sites that are able/willing to accept *F. japonica* waste, and so transportation to disposal facilities can be extremely costly. Only one waste disposal site in Cornwall will currently accept the material. This is located near Liskeard and is 57.4 miles from Penzance. It is estimated that a lorry will take around 4 hours for one round trip. This is at a cost of £30 per hour for a 20 tonne (net load capacity) lorry which could carry about 15 m³ of soil. The number of round trips required is thus given by ‘volume of soil / lorry volume capacity’ or ‘soil weight / lorry load capacity’ rounded up, whichever is the greater.

- **Tipping charges** This includes charges imposed by the specialist disposal sites required for *F. japonica* and any taxes that are applicable. Tipping charges can be highly variable; one site charging £35 per tonne whilst the site at Liskeard will cost over £200 per tonne. Landfill tax is currently £18 per tonne and will rise by £3 per tonne each year from 2005 onwards. However, in some regions this tax is waived by Customs and Excise for the disposal of *F. japonica* waste. The current price quoted
for the Liskeard site is £232.70 per tonne inclusive of landfill tax but excluding VAT (currently 17.5% in the UK)

- Relandscaping This includes filling in the hole created during excavation and any subsequent landscaping. This is estimated to cost around £5 per cubic metre.

These costs are summarised in Table 3.2. The difference in the cost between the best and worst case scenarios is clearly significant.

<table>
<thead>
<tr>
<th>Item</th>
<th>Calculation</th>
<th>Min. cost</th>
<th>Calculation</th>
<th>Max. Cost</th>
</tr>
</thead>
<tbody>
<tr>
<td>Excavation</td>
<td>1 day</td>
<td>£300</td>
<td>2 days</td>
<td>£600</td>
</tr>
<tr>
<td>Transport</td>
<td>(\frac{109}{15} \times 4 \times 30)</td>
<td>£960</td>
<td>(\frac{1083\times242}{20} \times 4 \times 30)</td>
<td>£14,640</td>
</tr>
<tr>
<td>Tipping</td>
<td>109 \times 2 242 \times 232 70</td>
<td>£56,866.76</td>
<td>1083 \times 2 242 \times 232 70</td>
<td>£565,015.61</td>
</tr>
<tr>
<td>Landscaping</td>
<td>109 \times 5</td>
<td>£545</td>
<td>1083 \times 5</td>
<td>£5,415</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>£57,711.76</td>
<td></td>
<td>£585,670.61</td>
</tr>
</tbody>
</table>

Table 3.2 Summary of estimated costs of disposal for the present state of the subject stand located in the Penzance area. Note the much higher cost resulting from the more extensive rhizome growth.

These data are coupled with the simulation predictions for the standard parameter set (see Section 3.4.1) with the maximum depth to which rhizomes may grow, \(h_{\text{max}}\), modified to account for the minimum and maximum volume scenarios. To calculate the minimum cost, the mean (over 10 trials) simulated area expansion for \(h_{\text{max}} = -0.9\) was used. Similarly, to calculate the maximum cost, the mean (over 10 trials) simulated area expansion for \(h_{\text{max}} = -3\) was used. Figure 3.15 shows how the mean (i.e., ignoring the model’s inherent variability) minimum and maximum cost for disposal might grow over the next 10 years according to the predictions of the correlated random walk model. These assume a constant inflation rate of 2% per year (rounded to nearest whole % and extrapolated from predicted consumer price inflation rates in [45]). If the volume to be disposed of was the minimum initially and rhizomes remain at most 0.9 m deep, costs should increase by approximately £40,116 (a 70% rise) in the next 10 years, excluding VAT. If the volume to be disposed of was at the maximum initially, costs could increase by as much as around £249,234 (43% increase).

The disposal costs associated with removing problematic stands of *F. japonica* can clearly be extremely high. The predicted increase in these costs demonstrated above represents a considerable financial burden for all concerned parties. Furthermore, the relatively short timescale in which such extra cost is incurred highlights the importance of dealing with infestations promptly.
Figure 3.15: Growth in stand area (top) and disposal costs (bottom) as predicted by the correlated random walk model for the minimum (left) and maximum (right) volume scenarios. The faster area expansion exhibited by the minimum volume scenario is due to the shallower depth limits meaning rhizomes tend to extend laterally more than vertically. Note that to dispose of waste in the maximum volume scenario is estimated to be an order of magnitude more expensive.
3.6 Discussion

In this section a 3D correlated random walk model for the development of a rhizome network in the invasive weed *F. japonica* was constructed. The collection and subsequent use of field data (detailed in Chapter 2) in the parameterisation and validation of the modelling features strongly in this work and extensive study of the effects of the few remaining unknown parameters on the crown density and rate of stand area expansion was undertaken. The simulation demonstrated that the model solutions are robust to changes in parameters, in that a small parameter change only leads to a small quantitative change in results.

For the standard parameter set, it was found that $a = 0.0035$. Since this figure is based on temporal increments of 4 months (one third of a year), this is equivalent to saying that $A \sim 9aY^2 = 0.0315Y^2$ where $Y$ is in full years. Experience suggests that this value may be somewhat low for real situations, something that remains to be shown through further fieldwork. However, it should be emphasised that this prediction is for the idealised situation in which the stand is not subject to any external influences such as human disturbance, environmental conditions, weather and so on. These factors all may introduce varying degrees of disturbance in the field, something that is well-known to encourage the plant's spread. This shows just how important some of these external influences might be in the plant's dispersal rate.

Modelling the development of a rhizome network at a single clone scale necessitates the use of the third dimension. Although some exceptional stands can grow to over 200 m$^2$ in area, 30–100 m$^2$ is more typical and at this scale the third dimension still plays a significant part in its development. Furthermore, the use of the third dimension in the correlated random walk is essential if the obtained field data, which was itself gleaned from a 3D structure, is to be utilised. Its inclusion not only represents the biology more closely, but key measurable data such as branching angles and segment lengths would be rendered irrelevant in a 2D model. Finally, 3D growth allows the rhizomes to circumnavigate obstacles in an inhomogeneous environment. The modular formulation of the simulation code allows for easy implementation of barriers to growth if required. Some of these are zero-flux (i.e. impenetrable) in nature, which may (e.g. walls and fences) or may not (e.g. a road) generally be negotiable by the plant, but others may only affect growth rates (e.g. poor or very dense substrate). The ability to overcome these impediments as the plant does in the wild is crucial to the formulation of a realistic model.

The correlated random walk model discussed in this section accurately predicts many of the field observations from this study. Since the field data features so heavily in the model, the simulations are able to produce realistic maps of a rhizome network's structure.
such it serves as a useful basis for more complex models in terms of a model free from any external influences such as management techniques, rhizome fragment transport in riparian environments or predation. The model could be used to predict the spread rates of existing stands or of new clones and also facilitates the estimation of biomass for a specific stand, although further investigation of the variability in rhizome diameters may be necessary here. Management of *F. japonica* infestations can be extremely costly and it would therefore be useful in the prioritisation and economic viability assessment of sites for treatment. An example of how the model predictions might be used for such a purpose is demonstrated in Section 3.5. Here, the potential costs of disposing of a problem stand of *F. japonica* according to the model predictions exhibit considerable increases over the relatively short timespan of 10 years. A similar study (requiring modification to the model to account for the ongoing effects of treatment) could also be undertaken for a programme of herbicide treatment. This is likely to be cheaper overall but is a long-term method of management, whereas the excavation of the entire stand and burial at a specialist site is immediately effective.

There exists a wide scope for extending this work further. Firstly, further field data is highly desirable in developing the model. Cam [13] reports a wide variation in the clonal growth parameters (branching angles, rhizome lengths and number of daughter rhizomes) between different sample sites for *S. altissima*. The same is likely to be true for *F. japonica*, suggesting that an area for further research would be the collection of equivalent data to that used in this report from different habitat types. The areas sampled were representative of a typical roadside verge/woodland habitat. The fieldwork in Cornwall was carried out on the periphery of a large stand and studied relatively young crowns and rhizomes. Older rhizomes are known to grow to a much larger diameter and it would be interesting to compare their properties with the newer growth. The soil also contained a lot of dumped material such as slate, rubble, glass bottles and so on which is a typical feature of the way in which *F. japonica* is spread by human activity, particularly fly-tipping. However, it only represents a single sample stand from a single habitat type. There are many different environments in which *F. japonica* may be found, e.g., sand dunes or river gravel, and it is reasonable to assume that its behaviour might be different in each. As well as the habitat type, environmental conditions such as pH values, availability of water, soil stability, water-tables, mineral content, altitude, sources of light and competition vary considerably and all play a significant part in the performance of the plant. It would be interesting to see how data from this study compare with those from sites featuring variations in any of these factors. As mentioned above, the properties of the long time spread on a larger scale may be determined from this model and so the investigation of field spread rates would
therefore be extremely useful, particularly in validating the quadratic expansion in time of the stand area predicted by the CRW model. It would also facilitate the assignment of an appropriate value to $\alpha$, which could then be referenced against the parameter surveys to select appropriate parameter values for those that remain unknown. At present such data is not readily available. However, a current study by CABI Biosciences in Switzerland (see [29]) should yield results relevant to this validation and should produce future collaborative work. Further field data may also be of use in a number of other ways. For example, given equivalent data to that currently used and possibly some small modifications, the model could be used to compare the development of the different varieties of $F. japonica$ (e.g., $F. japonica$ var. compacta or $F. japonica$ var. sachalinensis), hybrids such as $F. japonica$ x bohemica or even completely different clonal species exhibiting vegetative growth such as Solidago altissima (goldenrod), Arundo donax (giant reed) or Rubus fruticosus aggregate (blackberry).

Work on the model itself and its predictions may also be extended in a number of ways. Hormonal signals play a major role in the control of apical dominance, branching and crown formation. At present these features are modelled phenomenologically and a more biologically accurate mechanism could be included for such hormonal control. Another area for further development of the model would be to include the effects of some of the management techniques employed to control the spread of $F. japonica$. Of particular interest here would be the effects of different herbicides or a future biocontrol agent. The inclusion of heterogeneous habitats such as physical barriers to growth and lower quality substrate could be achieved by the introduction of spatially dependent parameters that vary in different regions of the domain. At present this has been included in a simple manner for the reaction-diffusion model described in Section 4.2 and could be included in a similar way for the CRW model. Additionally, minor modifications to the programme code would allow it to incorporate the habitat topology, such as hills and slopes. The results of the fieldwork in the second survey (Section 2.3.3) show that the new rhizome growth can be highly variable in length, suggesting that variable step-lengths during the correlated random walk might be a suitable adaptation of the model. Finally, the CRW model predicts expansion of stand area that is quadratic in time. Another widely-used class of model known as reaction-diffusion models also predict such expansion in area for large time. The use of a specific reaction-diffusion equation (the Fisher equation) as the basis for modelling the spatial spread of stands of $F. japonica$ on larger spatial and temporal scales is discussed in Chapter 4.
Chapter 4

Modelling the Spatial Spread of Aerial Stems in *F. japonica*: Larger Scales and Riparian Habitats

4.1 Introduction

The correlated random walk model for the development of the subterranean rhizome network for *F. japonica* described in Chapter 3 seems to predict such field data as was obtainable for model validation well. However, the use of the model on larger time and spatial scales rapidly becomes computationally substantial due to the exponential increase in the number of calculations performed over time. Whilst modelling at a single stand scale is useful for many of the proposed applications of the model, it would also be beneficial to look at larger spatial scales such as a watercourse or a field \(O(100 \text{ m}^2)\) and above. Indeed, the case of infested watercourses is of particular interest as this is one of the habitat types in which the impact of the presence of *F. japonica* is ecologically most damaging. As a first step towards modelling this situation, Section 4.2 details the use of a reaction-diffusion model, the Fisher equation, to model the spatial spread of the aerial stems in a stand of *F. japonica*. Such a model is more efficiently solved than the correlated random walk model for larger spatial and temporal scales. The numerical solution of this model is then described in Section 4.3. A 1D model based on a reaction-diffusion equation that has been extended to incorporate the influence of a watercourse is then considered in Section 4.4. Simulation of the 1D riparian model is discussed in Section 4.6. Finally, the 1D riparian model is incorporated into the original simulation of the 2D Fisher model in Section 4.7 to form a compartmentalised simulation model for the spatial spread of a stand in riparian habitats.
4.2 A Reaction-Diffusion Model of Aerial Stem Dispersal

The 'logistic equation' is an example of a simple, single-variable population model used to model local population growth in the absence of any dispersal mechanism

\[ \frac{du}{dt} = ru \left( 1 - \frac{u}{k} \right) \]  

(4.1)

where \( u \) is the population density, \( t \) is time, \( r \) is the intrinsic growth rate of the species and \( k \) represents the carrying capacity of the species' habitat [11, 14, 47]. The carrying capacity represents a maximum limit to the population density brought about by limited resources within the habitat, meaning that the environment can only support a finite density of individuals [11, 14, 47]. Here, it is assumed that the environment is closed and homogeneous so that the carrying capacity, \( k \), will be taken as a constant.

A more complex model than the classical logistic equation is the reaction-diffusion model in which local dispersal is also accounted for along with the local growth, representing a natural extension of equations such as (4.1)

\[ \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + f(u) \]  

(4.2)

Here, \( f(u) \) is the growth ('reaction') term, \( \frac{\partial u}{\partial t} \) is the rate of change of the population density with time and \( D \frac{\partial^2 u}{\partial x^2} \) represents spatial movement in one dimension with a constant diffusion coefficient \( D \). Since classical diffusion is the dispersal mechanism assumed here, the spatial flux, \( J \), of the population is given by \( J = -D \frac{\partial u}{\partial x} \) [47]. Such models have been used for many applications in biology, medicine and chemistry. One specific reaction-diffusion model is known as the Fisher equation and, in 1D, takes the form

\[ \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + ru(1 - \frac{u}{k}) \]

where \( r \) is the intrinsic growth rate of the subject species and \( r, D > 0 \). The Fisher equation was proposed by Fisher [26] as a model for the spatial spread of a favoured gene in a population. Note that long-distance dispersal events, such as wind-borne seed dispersal, are excluded from this model. The Fisher equation is very well-studied and is known to predict a constant wavespeed given by \( c \geq 2 \sqrt{rD} \) [47, 48] on an infinite domain. For initial conditions, \( u(x, 0) \), with compact support the travelling wavefront solution evolves to the solution with
the minimum wavespeed

\[ c_{\text{min}} = 2\sqrt{rD}, \]  

(4.3)
as described in [47]. The quadratic expansion in time of the area covered by a stand of *F. japonica*, as predicted by the correlated random walk (CRW) model in Chapter 3, is entirely consistent with the large time behaviour of the 2D Fisher equation

\[ \frac{\partial u}{\partial t} = D \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + ru(1 - \frac{u}{k}) \]  

(4.4)

Given the radial expansion velocity in equation (4.3), it may be deduced that the area

\[ A \approx \pi c_{\text{min}}^2 t^2 = 4\pi r Dt^2 \]  

Consequently, one can relate this to the CRW model with

\[ \alpha = 4\pi r D \]  

(4.5)

by comparison with equation (3.1). Thus, a model such as the Fisher equation should be a useful phenomenological equation for modelling stand expansion over long timescales and larger spatial scales than the CRW model (e.g., 10-100 m² or above) because it is computationally more efficient to solve in such circumstances. Given appropriate field data, the CRW model would allow the deduction of a realistic value for \( \alpha \), which can then be used to estimate the product \( rD \) (through equation (4.5)). This cannot be determined using the ‘snapshot’ data from this study which is based on fieldwork from a single visit.

Since *F. japonica* does not spread via seed dispersal in the UK, it is assumed that the spatial spread of the aerial stems of the plant may be modelled by a random walk process. Higgins and Richardson [33] give a review of different models of alien plant spread in which the suitability of reaction-diffusion models, amongst others, is assessed. They note some of the criticisms that have been made by various authors against the use of reaction-diffusion models for alien plant invasions and the simplifying assumptions that reaction-diffusion models make. It is suggested that, whilst reaction-diffusion models have enjoyed numerous successes at modelling the spread of animal species and diseases, they are perhaps less suited to alien plant spread. These criticisms (see [33] for specific references) include:

- The reaction-diffusion model is known to have been fairly successful at modelling the spread of certain animals and diseases, but is sometimes found to predict a rate of spread of up to an order of magnitude lower than observed in the field. This is thought to be due to using parameters that were estimated at lower hierarchical levels (e.g., from individuals) to model invasions at higher hierarchical levels (e.g., regional).
- The model takes no account of age/stage structure, its predictions of invasion speed
simply being a function of the growth rate $r$ and the diffusion coefficient $D$. Modifications to include the effects of age, reproduction and movement interactions were seen to improve the model's performance only slightly

- The model assumes that an invasion may be seen as a single expanding focus which is rarely seen in plant invasions.

- Few models of plant invasions have used reaction-diffusion models, even though they have been relatively successful in a number of applications to the spread of animals and disease. In one example the model was applied to the spread of postglacial oak trees in England, but was shown to be useful only in determining that something additional was responsible for the spread rate observed (a secondary disperser of the seeds). In another example the model was applied to the spread of a number of species of tree in the British Isles in order to estimate their diffusivity. The spread rate predicted by the model was found to be unrealistically high, suggesting that the species modelled were not subject to single focus spread.

- The model predicts that the square root of the area that the invader covers should increase linearly with time. The slope of this line should correspond to the mean wave-speed of the invasion. Neither of these two criteria were met under an experiment to test the reaction-diffusion model at modelling an invasion of *Mimosa pigra* in Australia.

- It is suggested that some of the underlying assumptions made by the reaction-diffusion model are unreasonable when modelling plant invasions. An example of this might be in that the model assumes normally distributed dispersal distances, whereas many wind/animal-dispersed plants actually have strongly leptokurtic (i.e. exhibiting high kurtosis with a higher ‘peak’ and thicker tails than the normal distribution) distributions. Also, some plants are dispersed via more than one means, which means that extra diffusion coefficients may be required.

- Modifications to a PDE model can be complicated and hence the addition of stochasticity, to account for such things as rare long-distance dispersal events, to the model may be difficult. This could be one reason why the model sometimes underestimates invasion rates.

- PDEs are said to be unsuitable for cases where dispersal is directed (e.g. via some form of taxis) and not random, and also for where heterogeneity in the environment affects the dispersal (e.g. a prevailing wind for seed-dispersed plants).
However, the arguments presented are less applicable in the context of this work than in other uses of the model. Its application here is on a relatively small scale and is not concerned with the large-scale invasion itself but with the expansion of individual stands. Given the plant's solely vegetative spread, it is not affected by external factors such as wind that might otherwise have enhanced seed dispersal and hence introduced some directional bias. In non-riparian habitats and in the absence of human disturbance, incidences of long-distance dispersal are also rare to non-existent. More importantly, the Fisher equation is used here on a purely phenomenological basis and therefore the underlying assumptions of the model are less important than the spread rate it predicts. Indeed, the results discussed in Section 3.6 and above further support the use of a Fisher-type model as a phenomenological representation of stand expansion due to its prediction of a constant wavefront speed given by equation (4.3). Should the prediction of area expansion being quadratic in time prove to fit field data well for individual stands, the Fisher equation should be a reasonable choice of model for predicting area expansion after all.

The assumption is made that *F. japonica* undergoes traditional logistic growth in crown formation. Also, since the observed crown density (see Chapter 2) was around 1 crown/m², *k* = 1 crown/m² is taken for the carrying capacity. Thus, the following two-dimensional Fisher equation is taken to model the spatial spread of the aerial stems:

\[
\frac{\partial u}{\partial t} = \nabla (D \nabla u) + f(u) = D \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + ru(1 - u),
\]

where the first term on the right-hand side of the equation represents the spatial spread of the plant in the *x* and *y* directions, whilst the second term represents its natural local growth as discussed previously in this section.

### 4.3 Numerical Simulation of the Fisher Equation

A simulation of the solution of the 2D Fisher equation (4.6) was programmed in Matlab. The solution domain is approximated by a grid *L* nodes in width by *H* nodes in height. These are separated by a distance *l* and *h* respectively (see Figure 4.1, left). Gridpoints were indexed from top to bottom, then left to right. This method of indexing was chosen to simplify the coding of the simulation since various Matlab functions require conventional matrix addressing to make correct use of the data. Thus, let the value of *u*(*x*, *y*, *t*) at a time *t* and at spatial point *P* on the grid be denoted by *u* *i j*, where *i* = 1, 2, ..., *H* and *j* = 1, 2, ..., *L*. The initial condition is a single point at the centre, while the boundary is set to zero.
\[ j = 1, 2, \ldots, L \] relate to the \((x, y)\) coordinates as shown in Figure 4.1. This means that \(u_{i-1,j}, u_{i+1,j}, u_{i,j-1}\) and \(u_{i,j+1}\) represent the values above, below, to the left and to the right of \(u_{i,j}\) respectively. These, along with \(u_{i,j}\), make up the 'finite difference molecule' (Figure 4.1, right).

On a discretized domain such as this, the spatial derivatives in the 2D Fisher equation (4.6) may be approximated by using finite differences [52] where

\[
\frac{\partial^2 u}{\partial x^2} \approx \frac{u_{i,j-1} - 2u_{i,j} + u_{i,j+1}}{l^2}
\]

and

\[
\frac{\partial^2 u}{\partial y^2} \approx \frac{u_{i-1,j} - 2u_{i,j} + u_{i+1,j}}{h^2}
\]

The temporal derivative is then represented by its forward difference approximation,

\[
\frac{\partial u}{\partial t} \approx \frac{u_{i,j}^{t+1} - u_{i,j}^t}{\Delta t}
\]
so that the explicit finite difference scheme

\[ u_{i,j}^{t+1} = \Delta t D \left( \frac{u_{i,j-1}^t - 2u_{i,j}^t + u_{i,j+1}^t}{l^2} + \frac{u_{i-1,j}^t - 2u_{i,j}^t + u_{i+1,j}^t}{h^2} \right) \]

(47) + \Delta t u_{i,j}^t (1 - u_{i,j}^t) + u_{i,j}^t

is obtained. It is well known (see, for example, [44] for proof) that the stability of such a scheme is guaranteed for

\[ D \Delta t \left( \frac{1}{l^2} + \frac{1}{h^2} \right) \leq \frac{1}{2} \]

(48)

The finite difference equation (47) for solving the Fisher model is a very well studied scheme and requires no further elaboration here, although stability analysis that is applicable to such a scheme is discussed in Section 4.7 for a similar scheme with some additional components.

Initially the model was simulated on a rectangular homogeneous domain, the boundaries of which were taken to be zero-flux, \( u_x(0, y) = u_x(L_x, y) = 0 \) and \( u_y(x, 0) = u_y(x, H_y) = 0 \), where \( L_x = l(L - 1) \) and \( H_y = h(H - 1) \) are the domain width and height in real space. Noting that the finite difference approximations for \( \frac{\partial u}{\partial x} \) and \( \frac{\partial u}{\partial y} \) are

\[
\frac{\partial u}{\partial x} \approx \frac{u_{i,j+1}^t - u_{i,j-1}^t}{2l}, \\
\frac{\partial u}{\partial y} \approx \frac{u_{i+1,j}^t - u_{i-1,j}^t}{2h},
\]

and imposing the zero-flux boundary conditions, it may be deduced that \( u_{i+1,j}^t = u_{i-1,j}^t \) for \( x = 0, L_x \) and \( u_{i,j+1}^t = u_{i,j-1}^t \) for \( y = 0, H_y \). Thus, for any points at the boundary at which one or more points of the finite difference molecule lie outside the boundary, the corresponding value from the opposing side of the finite difference molecule may be substituted.

Figure 4.2 shows how the simulated solution develops over time. For initial conditions in which a single fragment of rhizome is introduced to the otherwise empty domain (i.e. \( u(40,50,0) = 1 \) and \( u(x,y,0) = 0 \) elsewhere in the figure), a single expanding circular stand is formed as expected. This basic simulation programme was then extended to include a number of advanced features. These are described below.

**Advanced simulation features**

The use of a 2D reaction-diffusion model was motivated by the need for a tool to demonstrate how a stand of *F. japonica* might look in the future if left to grow naturally with no human intervention. For this to be achieved, a number of advanced features needed to be implemented in the simulation of the Fisher model to enhance its capabilities as a useful and
Figure 4.2: The simulated solution to the Fisher model for $L = 201$, $H = 161$, $l = h = 0.5$ and $\Delta t = 0.01$ (so that the stability criterion (4.8) is satisfied). Areas of higher population density are red whilst the lower population densities are blue.
versatile tool. The major features added include the following:

- The ability to run the simulation on a geographical map incorporating a custom domain. A facility to underlay any background image in the Matlab figures enables the simulation of stands on arbitrary maps depicting hypothetical or physical geography. This means that specific infestations in the field may be studied and predictions made as to their future properties. Of course, the terrain displayed on such a map may not be homogeneous in nature. They may feature roads, buildings, watercourses and other terrain types that act as barriers or impediments to the spread of *F. japonica*. It was therefore necessary to include the facility to define custom domains in which the plant may grow. These two features are illustrated in Figure 4.3. Here, a dockland map (modified from a map of the Alexandra Dock, King’s Lynn) is shown in which the (fictional) area that is viable for plant growth has been manually defined (shown in blue). Roads and concrete areas are shown in black and water in dark grey. This is achieved via the use of Matlab’s ‘ginput’ function which allows one to click on a displayed figure with the mouse to input the coordinates of a point. Using this function makes it possible to easily define domains that are specific to any particular map.

![Figure 4.3: The ability to define custom domains was added to the simulation programme. A manually-defined domain is shown here in blue, water is shown in dark grey and roads an concrete areas are shown in black.](image)

An extension of this feature added to the programme but not further developed in this study (*k* = 1 is assumed throughout this work) is the ability to include multiple patches of lower fertility. This was implemented by simply setting areas of the domain a lower carrying capacity *k*, achieved by using Matlab’s ‘ginput’ function. This feature could
be used, for example, to phenomenologically represent areas of the map with different environmental factors such as differing substrate types, light availability, competition levels and so on.

- User-definable initial conditions including automatic extraction from existing data. Matlab's 'ginput' function was also used in a similar fashion to that used for the custom domains discussed above to plot and use arbitrary initial conditions on the map. An example of the use of this feature is shown in Figure 4.4. Here, the dockland map mentioned above has had three arbitrary stands of *F. japonica* plotted on it. The programme can then use these as initial conditions in the simulation.

![Figure 4.4: Coloured patches here represent the shapes of 3 manually-defined stands of *F. japonica* that are used as initial conditions in the simulation.](image)

This feature is extended further by incorporating the option to have the programme automatically process an image in order to extract the initial conditions without the need for manual input. This feature is particularly useful when data from a geographical information system (GIS) is being considered. Figure 4.5 illustrates such a case. Here, a sample of the GIS data collected in the Swansea surveys (to be detailed further in Section 4.4.1) shows the location and shape of a stand of *F. japonica* in Swansea (UK) in 1998. The map is automatically processed by the programme to extract the shape of the stand that may then be used as initial conditions. It is first passed through a colour filter, retaining only the data relating to the stand itself. The resulting array storing the colour data is then easily converted into the required form for use in the simulation.

Thus, initial conditions, physical barriers and regions of lower substrate fertility such as might exist in the field may be predefined on the subject domain before the solution of the
Figure 4.5: The code contains an automatic map-processing facility to extract initial conditions. A map containing, for example, GIS data on stand locations (left) may be converted automatically into an array storing only the relevant information to construct the initial conditions (right). GIS data supplied by the City and Council of Swansea.

governing equations is carried out. Once these are entered the solution is then calculated according to the preset parameters. In this example \( r = 1 \) and \( D = 1 \) are taken purely for demonstration purposes. Figure 4.6 shows frames from the resulting simulation output movie, using the initial conditions shown in Fig. 4.4 on the domain shown in Figure 4.3. Using the rate of area expansion \( \alpha \), as calculated for the standard parameter set in Section 3.4.1, the distance travelled \( d^* \) by the wavefront from a point \( d_0 \) in time \( t \) is given by \( d^* = d_0 + \sqrt{\alpha t} \). This was used to calculate the approximate dimensional time intervals between the output frames shown (see Figure 4.6 for details). Although the spatial scale of these maps is relatively large, the predicted times to attain the stand sizes shown appears to be somewhat high. This is perhaps due to \( \alpha \) being lower than might be expected in the field, as discussed in Section 3.6.

The simulation programme discussed here is used as the basis for a more complex programme presented in Section 4.7, which also includes a more detailed account of the simulation procedure. The exact procedure for this particular programme is thus omitted here. However, it is clear that the programme displays a great deal of potential as a predictive tool on terrain that could be considered homogeneous and free from external influences. However, \( F. japonica \) is commonly found in riparian habitats where the presence of a watercourse can significantly aid its rate of spread. This effect is discussed in Section 4.4 and is modelled via a 1D advection model along the banks of a watercourse. This model is then combined
Figure 4.6: Simulation output movie frames at predicted dimensional times \( t \approx 0, 76, 190, 304 \) years for the initial conditions depicted in Figure 4.4. Note the effect of the boundaries marked in Figure 4.3. Image widths are approximately 445 m.
with the Fisher model presented in this section to produce a compartmentalised 2D model for the spatial spread of *F. japonica* in riparian habitats.

### 4.4 Modelling Dispersal in Riparian Environments

In this section the spatial spread of *F. japonica* in a riparian environment is modelled by extending the Fisher model discussed in Sections 4.2 and 4.3 to include terms for the loss of plant fragments to the watercourse and the subsequent transport downstream and washing up to regenerate into fresh clones. The background and motivation for this is discussed in Section 4.4.1 and model equations are formulated in Section 4.4.2. Boundary and initial conditions are discussed in Section 4.4.3 and the model equations are then nondimensionalised and simplified in Section 4.4.4.

#### 4.4.1 Background and Motivation

Documented and anecdotal accounts of the rapid downstream spread of *F. japonica* along the banks of watercourses are numerous. Examples of evidence for the phenomenon include the following:

- The effect is hinted at in the quotation of Cathy Lucero given in Section 1.6 as being one of the causes of large monocultures along the banks of watercourses in Washington State, USA.

- Figure 4.7 illustrates the banks of a stream that have been completely overrun with *F. japonica*. This is a common sight along infested watercourses.

- Figure 4.8 shows a similar situation but on a much larger scale. The Geographical Information System (GIS) data (provided by New York City Department of Environmental Protection) depicts the location of large monocultures along the Batavia Kill stream corridor, a tributary of the Schoharie Creek in the water supply watershed of the city of New York, USA.

- Talmage and Kiviat [55] state that

  The commonest mode of dispersal in both the U.K. and North America is by water transportation of plant fragments.

This is supported by Child *et al.* [19] who state that the fragments are carried downstream by high water flows. The phenomenon is also mentioned in a number of other publications (see, for example, [32, 50]).
Figure 4.7: A typical invasion in a riparian environment. Both sides of the stream have been completely overrun with *F. japonica*. Picture courtesy of Sean Hathaway, City and Council of Swansea.

Figure 4.8: Left: The Batavia Kill stream corridor near the city of New York, USA. Map obtained from the software package Google Earth. Right: GIS data of a large-scale riparian invasion on the Batavia Kill. Note the presence of *F. japonica* (grey patches) along the entire length of this section of the watercourse. Image width approximately 8 miles (12.8 km). Data courtesy of New York City Department of Environmental Protection.
In 1992 a survey of the spatial distribution of *F. japonica* in Swansea (Wales) was undertaken on behalf of the City and Council of Swansea (see [16, 19, 32, 59]). This information was transferred to a GIS, facilitating the monitoring of stand development over time. A second survey was undertaken in 1998 using the same methodology but covering a slightly larger area. Data from the two surveys were then directly comparable, showing how individual stands had expanded over time as well as larger scale properties of the infestation. Figure 4.9 shows two examples of the resulting data which appear to support the notion of faster spread along the banks of a watercourse. It should be noted, however, that the direction of flow is not known for certain for these data. The geographical proximity of Washinghouse Brook (top) to Swansea Bay suggests that the direction of flow in this case is from West to East. Similarly, the geographical location of the Clyne River (bottom) suggests that the direction of flow is likely to be from North to South. If these assumptions are true, the *F. japonica* on both sites has actually spread fastest in the upstream direction (although downstream spread is blocked by what appears to be a road or path in both examples and the application of any previous management is unknown). A possible explanation for this behaviour may be drawn from the modelling work to be discussed in Section 4.4.2 onwards.

Brock and Wade [10] highlight the fact that in riparian habitats where mechanical cutting of stands is used, the water plays a significant role in the dispersal of scattered stem fragments. As well as stem fragments falling into watercourses, human-induced scattering, changes in water-level and flooding events can cause rhizome fragments to enter the flow [17]. Brock and Wade [10] also investigate the regenerative properties of *F. japonica* from rhizome and stem fragments in controlled greenhouse trials. They found that stem fragments that were left to float in water alone proved to be the most likely to regenerate. Rhizome fragments as small as 0.7 g were found to generate new shoots [10]. Overall they found that 69% of their rhizome samples produced stem shoots and 86.6% produced new root material. This constitutes direct evidence of the high viability of plant fragments for regeneration and the development of new stands.

The transport of waterborne stem and rhizome fragments coupled with their high viability for regeneration is clearly a significant factor in the spread of *F. japonica* in riparian habitats and is thus an important process to include for modelling the problem in such environments. As a first step, a 1D model of events occurring along a river bank is considered in Section 4.4.2. Simulation of the model is then detailed in Section 4.6. This is then incorporated into the 2D simulation presented in Section 4.3, as described in Section 4.7.
Figure 4.9: Data from the Swansea surveys shows how *Fallopia japonica* has spread from 1992 (left) to 1998 (right) in the area. These two examples show riparian habitats. Top: Washinghouse Brook, near Westcross Lane, Swansea (approx. Lat: 51:35:14N, Lon: 4:00:02W). Bottom: Clyne River, Clyne Valley Country Park, Swansea (approx. Lat: 51:36:09N, Lon: 4:00:05W). Note the apparent tendency to spread more quickly along the banks of the watercourse. Approximate image widths: top 125 m, bottom 180 m.
4.4.2 Model Equations

Figure 4.10: A schematic of the riparian model. 1: Fragments of the plant’s (yellow) stem and rhizome fall into the water close to the bank (red). 2: The watercourse transports them downstream. 3: Some fraction of the waterborne population enters the faster flow (blue) in the middle of the watercourse due to mixing, whilst some of it remains close to the bank. 4: Some of the waterborne population that was lost to the middle of the watercourse may re-enter the near-bank flow or be lost to the system permanently by being washed out. 5: Fragments may be washed back up on the bank where they can form a new stand.

Figure 4.10 illustrates a schematic of the proposed model. *F. japonica* grows and spreads as discussed previously for the Fisher model until it reaches the bank of the watercourse. Here, fragments of stem and rhizome are deposited in the flow. They are then washed downstream and subsequently may either be washed out of the system entirely or be washed up on the bank to regenerate into a fresh clone. Some of the waterborne population that was washed out of the system returns to it as a result of mixing transverse to the direction of flow.

A general reaction-diffusion model is considered as a starting point for a model of the spatial spread of the aerial shoots along the bank of a watercourse:

\[
\frac{\partial u_b}{\partial t} = D \nabla^2 u_b + f(u_b, u_w),
\]  

(4.9)

where \( u_b(x, t) \) is the population density of the plant resident on the bank domain, \( \Gamma \), and \( u_w(x, t) \) represents the population density of plant fragments present in the watercourse flow close to the bank. Spatial spread on \( \Gamma \) is incorporated by assuming diffusive spread with constant diffusivity, \( D \), and local growth by the reaction term, \( f(u_b, u_w) \). It is required that \( f(u_b, u_w) \) satisfies \( f(u_b, 0) = ru_b(1 - u_b) \), which is the same as that discussed in Section 4.2, and that \( u_w \) enhances the growth rate without increasing the carrying capacity. Thus, for simplicity

\[
f(u_b, u_w) = (ru_b + \psi u_w)(1 - \frac{u_b}{k})
\]

is chosen, where \( k = 1 \) crown/m² is assumed henceforth as before and the \( \psi u_w \) term governs
the enhanced growth due to the deposition of rhizome fragments from the watercourse on to
the bank and their subsequent regeneration. In 1D space, equation (4.9) therefore becomes
the following model for the spread of *F. japonica* on the bank

\[
\frac{\partial u_b}{\partial t} = D \frac{\partial^2 u_b}{\partial x^2} + (ru_b + \psi u_w)(1 - u_b)
\]

For the waterborne population, no growth occurs and the domain is fed by fragments of
plant falling/being washed into the water. A small proportion of these are washed up on to
the bank and thus are lost to the water. Fragments are also lost by drifting into the middle
of the river and thereby being ‘washed out’ of the system. However, there is always the
chance of such washed out fragments returning to the system further downstream. Thus,
the following model is considered for the waterborne population:

\[
\frac{\partial u_w}{\partial t} = \gamma u_b - v \frac{\partial u_w}{\partial x} - \psi u_w - \beta u_w + \rho \int_0^\infty K(\xi)u_w(x - \xi, t - \xi/v) d\xi
\]  

(4.10)

Here, \(\frac{\partial u_w}{\partial x}\) is the advection along the river, \(v\) represents the speed of water flow and \(\beta\) is the
rate at which fragments are lost (washed out) to the system. The final term on the right-hand
side of equation (4.10) is a ‘return function’ representing the return of washed out fragments
to the system at some rate \(\rho\). Here, \(K(\xi)\) is the return function kernel, proportional to the
probability of a fragment of plant being washed out at a distance \(\xi\) upstream and returning to
the system at \(x\). Over the area of interest (\(O(100\ m)\)) it is assumed that the flow properties
of the river remain largely unchanged so that parameters \(v, \psi, \beta, \rho\) are all approximately
constant. Thus, the following system is obtained

\[
\frac{\partial u_b}{\partial t} = D \frac{\partial^2 u_b}{\partial x^2} + (ru_b + \psi u_w)(1 - u_b)
\]

(4.11)

\[
\frac{\partial u_w}{\partial t} = \gamma u_b - v \frac{\partial u_w}{\partial x} - \psi u_w - \beta u_w + \rho \int_0^\infty K(\xi)u_w(x - \xi, t - \xi/v) d\xi.
\]

with

\[0 < t \leq T, \quad x \in \Gamma,\]

where

\[\Gamma = \{x \in (-\infty, \infty)\}\]

and where \(f(u_b, u_w)\) is continuous and differentiable on \((u_b, u_w) \in [0, 1]\) and satisfies

\[f(0, 0) = f(1, u_w) = 0\]

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In the forthcoming analysis the infinite domain is used, as given above. However, for the numerical simulation discussed in Section 4.6 a domain of 10,001 nodes (2500 units) is generally used, unless otherwise stated, as an approximation to the infinite domain.

### 4.4.3 Boundary and Initial Conditions

The system (4.11) is subject to the following initial and boundary conditions:

\[
\begin{align*}
    u_b(x, 0) &= u^0(x), \\
    u_w(x, 0) &= 0, \\
    u_b(x, t) &= 0, \quad x \in \partial \Omega, \\
    u_w(-\infty, t) &= 0
\end{align*}
\]

### 4.4.4 Nondimensionalisation and Model Simplification

The system (4.11) is nondimensionalised using

\[
\begin{align*}
    t^* &= rt, \quad x^* = x\sqrt{r/D}, \quad \psi = r\psi^*, \quad \gamma = r\gamma^*, \quad u_w = \frac{r}{v} u_w^*, \\
    \beta &= r\beta^*, \quad \xi^* = \sqrt{rD}\xi, \quad v = \sqrt{rD}v^*, \quad \rho^* = \frac{\rho}{r\sqrt{rD}}, \\
    u_b(x, t) &\rightarrow u_b^*(x^*, t^*), \quad u_w(x, t) \rightarrow u_w^*(x^*, t^*)
\end{align*}
\]

and dropping asterisks for convenience yields

\[
\begin{align*}
    \frac{\partial u_b}{\partial t} &= \frac{\partial^2 u_b}{\partial x^2} + (u_b + \frac{\psi\gamma}{\nu} u_w)(1 - u_b) \\
    \frac{1}{\nu} \frac{\partial u_w}{\partial t} &= u_b - \frac{\partial u_w}{\partial x} - \frac{\psi + \beta}{\nu} u_w + \frac{\rho}{\nu} \int_0^\infty K\left(\frac{\xi}{\sqrt{rD}}\right) u_w\left(\frac{x - \xi}{\sqrt{rD}}, \frac{1}{r}(t - \frac{\xi}{Dv})\right) d\xi
\end{align*}
\]

The expansion of a stand of *F. japonica* occurs on a timescale of \(O(m/\text{year})\) which is considerably slower than the flow of the watercourse. It is therefore expected that \(v \gg 1\). Furthermore, it is expected that the majority of the rhizome fragments entering the flow will be lost and that those that do return to the bank exhibit a high viability for regeneration. Thus, it is also assumed that \(\mu = \frac{\psi\gamma}{\nu}\) and \(\beta_0 = \frac{\beta + \gamma}{\nu}\) are \(O(1)\) quantities. So taking \(v \rightarrow \infty\)
the system simplifies to
\[
\begin{align*}
\frac{\partial u_b}{\partial t} &= \frac{\partial^2 u_b}{\partial x^2} + (u_b + \mu u_w)(1 - u_b) \\
\frac{\partial u_w}{\partial x} &= u_b - \beta_0 u_w
\end{align*}
\] (4.12)

### 4.5 Travelling Wave Analysis

In the simulations of the 1D riparian model (to be presented in Section 4.6) it was found that both the downstream and upstream wavespeeds are, under certain parameter regimes, enhanced by the influence of the watercourse. In order to understand these findings more comprehensively, we first consider the formal analysis here. In this section travelling wave analysis is carried out to investigate the effects of the key parameters in the simplified system (4.12), namely \(\beta_0\) and \(\mu\), on the predicted upstream and downstream wavespeeds.

#### 4.5.1 Spatially Homogeneous Steady States

In order to analyse the travelling wave solution it is necessary to establish the spatially independent steady states of the system. These will form the boundary conditions in the travelling wave analysis to follow in Section 4.5.2.

The spatially independent steady states are given by \((u_b, u_w) = (u_b^*, u_w^*)\) satisfying
\[
\begin{align*}
f_b(u_b^*, u_w^*) &= (u_b^* + \mu u_w^*)(1 - u_b^*) = 0, \\
f_w(u_b^*, u_w^*) &= u_b^* - \beta_0 u_w^* = 0,
\end{align*}
\] (4.13)

and are located at \((u_b^*, u_w^*) = (0, 0), (1, \frac{1}{\beta_0})\). The stability matrix for the system (4.13) is defined to be the Jacobian matrix of \(f_b(u_b, u_w)\) and \(f_w(u_b, u_w)\) at \((u_b^*, u_w^*)\), namely

\[
A = \begin{bmatrix}
1 - 2u_b^* - \mu u_w^* & \mu(1 - u_b^*) \\
1 & -\beta_0
\end{bmatrix}
\] (4.14)

The stability of each of the steady states can be established from the eigenvalues of \(A\) or, equivalently, from its trace and determinant (see [47], Appendix 1).

- For \((0, 0)\), the matrix (4.14) is

\[
A_0 = \begin{bmatrix} 1 & \mu \\ 1 & -\beta_0 \end{bmatrix},
\]

which has \(\text{tr}(A_0) = 1 - \beta_0\) and \(\text{det}(A_0) = -\beta_0 - \mu\). Imposing \(\beta_0, \mu > 0\) results in
\[ \det(A_0) < 0 \text{ implying that } (u_b, u_w) = (0, 0) \text{ is a saddle point} \]

- For the coexistence steady state \((1, \frac{1}{\beta_0})\), matrix (4.14) is

\[
A_c = \begin{bmatrix}
-1 - \frac{\mu}{\beta_0} & 0 \\
1 & -\beta_0
\end{bmatrix}
\]

Here, the eigenvalues are given by

\[
\lambda_1 = -1 - \frac{\mu}{\beta_0} < 0,
\lambda_2 = -\beta_0 < 0,
\]

both of which are negative and real implying that the steady state is a stable node.

The two steady states \((0, 0)\) and \((1, \frac{1}{\beta_0})\) will form the boundary conditions in the analysis to follow.

**4.5.2 Travelling Wave Analysis**

In this section, travelling wave analysis is undertaken in order to study the behaviour of the travelling wave fronts along the bank of the watercourse in both the upstream and the downstream directions. These two cases will be considered separately below.

In the absence of diffusion/advection, the steady states of the simplified system (4.12) are \((u_b, u_w) = (0, 0), (1, \frac{1}{\beta_0})\). The travelling wave solutions are assumed to connect these two steady states and are sought by looking for solutions of the system of the form \((u_b, u_w)(x, t) = (U_b, U_w)(z)\), where \(z = x - ct\) (see [47]). The system then becomes

\[
U''_b + cU'_b + (U_b + \mu U_w)(1 - U_b) = 0, \tag{4.15}
\]

\[
U'_w + \beta_0 U_w - U_b = 0, \tag{4.16}
\]

where \('\) denotes differentiation with respect to \(z\). For the downstream spread \((c > 0)\) the boundary conditions

\[
\lim_{z \to -\infty} U_b = 1, \quad \lim_{z \to \infty} U_b = 0, \quad \lim_{z \to -\infty} U_w = \frac{1}{\beta_0}, \tag{4.17}
\]

are imposed. Similarly, for the upstream spread \((c < 0)\) the boundary conditions

\[
\lim_{z \to -\infty} U_b = 0, \quad \lim_{z \to \infty} U_b = 1, \quad \lim_{z \to -\infty} U_w = \frac{1}{\beta_0}, \tag{4.18}
\]
are imposed. It will be shown later that these conditions are sufficient for a well-posed problem.

As with the standard analysis for the Fisher equation (see [47]), a bound on the wavespeed is sought by studying the behaviour of the linearised solution as $z \to \pm \infty$. Let $W_b = U'_b$ so that

\begin{align*}
U'_b &= W_b, \\
U'_w &= U_b - \beta_0 U_w, \\
W'_b &= U_b^2 + \mu U_b U_w - c W_b - U_b - \mu U_w
\end{align*}

It follows from the above steady state analysis that the steady states of these are at $(U_b^*, U_w^*, W_b^*) = (0, 0, 0), (1, \frac{1}{\beta_0}, 0)$ The stability matrix is then

$$A = \begin{bmatrix} 0 & 0 & 1 \\ 1 & -\beta_0 & 0 \\ 2 U_b^* + \mu U_w^* - 1 & \mu (U_b^* - 1) & -c \end{bmatrix}$$

The downstream and upstream cases will now be discussed separately.

**Downstream**

Consider first the wavefront travelling in the downstream direction ($c > 0$) As $z \to \infty$, the perturbation about $(0, 0, 0)$ leads to the stability matrix

$$A_0 = \begin{bmatrix} 0 & 0 & 1 \\ 1 & -\beta_0 & 0 \\ -1 & -\mu & -c \end{bmatrix},$$

which has the characteristic polynomial

$$P_0^+(\lambda) = \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3,$$

where the coefficients $a_i$ are given by

\begin{align*}
a_1 &= \beta_0 + c, \\
a_2 &= 1 + \beta_0 c, \\
a_3 &= \mu + \beta_0
\end{align*}
Using Descartes’ rule of signs (see [47]) it is possible to determine information on the sign of the roots of the characteristic polynomial (4.19) The coefficients \( a_1, a_2 \) and \( a_3 \) are all positive for \( c > 0 \) Hence, the number of changes of sign in equation (4.19) is zero Thus, there are no positive real roots Now let \( \lambda = -\omega \) so that (4.19) becomes

\[
\omega^3 - a_1\omega^2 + a_2\omega - a_3 = 0,
\]

which has three changes of sign and so (4.19) has either three real roots or one negative real root and 2 complex roots For the solution to be physically relevant it is required that \( U_b, U_w \geq 0 \) for all \( z \) Hence, oscillatory behaviour is not permitted due to the solution entering the negative region as \( z \to +\infty \) and the latter case may be disregarded Therefore, the value of \( c \) must be such that all three eigenvalues are real and negative

Let \( \Omega = 2(\frac{a_1}{3})^3 - \frac{a_2a_3}{3} + a_3 \) and \( \alpha = \frac{1}{3}(\frac{a_2}{3} - a_2) \) Then from Table A.2.1 in Murray [47], solutions of (4.19) are all real only when \( |\Omega| \leq 2\alpha^{3/2} \) Defining

\[
g_d(c) = \Omega^2 - 4\alpha^3 = \left(\frac{2}{27}(\beta_0 + c)^3 - \frac{1}{3}(\beta_0 + c)(1 + \beta_0c) + \mu + \beta_0\right)^2
- 4\left(\frac{(\beta_0 + c)^2}{9} - \frac{1 + \beta_0c}{3}\right)^3,
\]

where subscript \( d \) on \( g_d(c) \) denotes the downstream case, \( c \) may be sought such that \( g_d(c) \leq 0 \). Note that \( g_d(0) = \frac{4}{27}\beta_0^4 + \frac{4}{27}\beta_3\mu + \frac{8}{27}\beta_0^2 + \frac{4}{3}\beta_0\mu + \mu^2 + \frac{4}{27} > 0 \) and \( g_d(c) \to -\infty \) as \( c \to +\infty \) Therefore, by the continuity of \( g_d(c) \), there must at least be a value of \( c \), \( c^+_{\min} \), say, such that \( g_d(c) \leq 0 \) for \( c \geq c^+_{\min} \) Thus, \( c = c^+_{\min} \) represents the minimum wavespeed for which the solutions of (4.19) are all real Using equation (4.21) it is straightforward to calculate \( c^+_{\min} \), given values of \( \beta_0 \) and \( \mu \), as demonstrated below and in Section 4.6.1

Figure 4.11 (left) shows the solutions for \( g_d(c^+_{\min}) = 0 \) on \( \beta_0 \in [0, 1, 5] \) with \( \mu = 0.05, 0.2, 1, 5 \) and (right) the solutions for \( g_d(c^+_{\min}) = 0 \) on \( \mu \in [0, 1, 5] \) with \( \beta_0 = 0.2, 1, 5 \) Over the parameter ranges examined here, it is clear that the downstream wavespeed is affected by variations in magnitude of all \( \beta_0, \mu \in [0, 1, 5] \) However, as expected, the two parameters have opposing effects For increasing \( \beta_0 \), \( c^+_{\min} \) decreases monotonically and is bounded below by \( c = 2 \) (the minimum wavespeed predicted by the standard Fisher model) The physical interpretation for this is an increasing amount of biomass lost permanently to the watercourse such that the system tends to non-riparian spread rates due to a relatively small remaining waterborne population For increasing \( \mu \), \( c^+_{\min} \) increases monotonically, reflecting the greater incidence of fragment deposition and regeneration that contributes to
the population on the bank and enhances the wave propagation. The magnitudes predicted for the downstream spread are far in excess of those for the upstream wave (see below) for most parameter configurations. The most extreme example shown is for the case $\beta_0 = 0.2$, in which the downstream wavespeed increases extremely rapidly such that for $\mu = 0.2, 1, 5$, $c^+_{\min} = 29.26, 109.88, 510.05$ respectively (not shown in the figure for clarity). The physical interpretation here is that a relatively small proportion of the waterborne population are being lost to the system, resulting in a much larger waterborne population to be washed back up on the bank and regenerate. The contribution from the watercourse is therefore very significant in such cases.

![Graphs showing implicit solutions of $g_d(c^t_{\min}) = 0$.](image)

Figure 4.11: Implicit solutions of $g_d(c^t_{\min}) = 0$. Left: The solutions for $c^t_{\min}$ on $\beta_0 \in [0.1, 5]$ with $\mu = 0.05, 0.2, 1, 5$ (black, red, green and blue respectively). Right: The solutions for $c^t_{\min}$ on $\mu \in [0.1, 5]$ with $\beta_0 = 0.2, 1, 5$ (red, green and blue respectively).

Also worthy of note is the extra 'lower' solution that exists for small $\mu$, as shown in Figure 4.11 (left) for $\mu = 0.05$. Figure 4.12 shows $\tanh(g_d(c))$ (for clarity) against $c$ for $\mu = 0.05$ and $\beta_0 = 0.01$. This plot illustrates that there are two possible ranges of $c$ in which $g_d(c) \leq 0$ for small $\mu$ and $\beta_0$. Although the leftmost range, $c_1 \leq c \leq c_2$, appears to satisfy the criterion that $g_d(c) \leq 0$, examination of the eigenvector corresponding to the least negative eigenvalue, $\lambda^*$, yields

$$v_{\lambda^*} = \begin{pmatrix} \lambda^* + \beta_0 \\ 1 \\ \lambda^*(\lambda^* + \beta_0) \end{pmatrix}.$$
Figure 4.12: Semilog plot of $\tanh(g_d(c))$ against $c$ for $\mu = 0.05$, $\beta_0 = 0.01$ illustrating the two possible ranges, $c_1 \leq c \leq c_2$ and $c_{\text{min}} \leq c$, in which $g_d(c) \leq 0$.

Now,

$$\begin{pmatrix} U_b \\ U_w \\ W_b \end{pmatrix} = A_{\lambda, \beta}e^{\lambda^* z},$$

meaning that as $z \to \infty$ we require that $\lambda^* + \beta_0 > 0$ and $1 > 0$ (trivially satisfied) so that $U_b$ and $U_w$ remain positive for physically relevant solutions. Figure 4.13 shows a plot of $\lambda^* + \beta_0$ against $c$ for the case $\beta_0 = 0.2$ and $\mu = 0.05$. Here, it is clear that the plot corresponding to the lower solution in Figure 4.11 fails to satisfy $\lambda^* + \beta_0 > 0$. In this case, $c_1 = 1.93$ and $c_2 = 2.28$ so that for $c_1 \leq c \leq c_2$, the solution exists but $U_b \to 0^- < 0$ as $z \to +\infty$. Therefore, the lower solution for small $\mu$ is only valid for the non-physical case with negative population densities. It is thus disregarded hereafter.

For completeness, consider now the coexistence steady state. As $z \to -\infty$, the perturbation about $(1, \frac{1}{\beta_0}, 0)$ leads to the stability matrix

$$A_c = \begin{bmatrix} 0 & 0 & 1 \\ 1 & -\beta_0 & 0 \\ 1 + \frac{\mu}{\beta_0} & 0 & -c \end{bmatrix},$$
Figure 4.13: \( \lambda^* + \beta_0 \) (y axis) against \( c \) (x axis) for \( \beta_0 = 0.2 \) and \( \mu = 0.05 \). In this case, \( c_1 = 1.93 \) and \( c_2 = 2.28 \). The red lines correspond to the two solutions depicted in Figure 4.11 (left) for \( \mu = 0.05 \), the left corresponding to the lower solution and the right to the upper solution.

which has the characteristic polynomial

\[
P_c^+ (\lambda) = (-\beta_0 - \lambda)(\lambda(c + \lambda) - (1 + \frac{\mu}{\beta_0})).
\]

Solving yields

\[
(-\beta_0 - \lambda)(\lambda(c + \lambda) - (1 + \frac{\mu}{\beta_0})) = 0,
\]

\[
\Rightarrow (\beta_0 + \lambda)(\lambda^2 + c\lambda - (1 + \frac{\mu}{\beta_0})) = 0,
\]

\[
\Rightarrow \lambda = -\beta_0, \quad \lambda = -\frac{c}{2} \pm \frac{\sqrt{c^2 + 4(1 + \frac{\mu}{\beta_0})}}{2}.
\]  \hspace{1cm} (4.22)

There are therefore two negative and one positive eigenvalues for the perturbation about the coexistence state. Since the eigenvalues are real, there will not be any oscillatory behaviour behind the wave.

In the interests of ensuring the well-posedness of the problem described by equations (4.15) and (4.16) it is required that the total number of stable eigenvalues at both ends of the domain is equal to the number of boundary conditions plus one extra to account for the translational invariance (i.e. the translation of the spatial coordinate, for example \( z = z^* + \alpha \) where \( \alpha \) is some constant, results in no change to the solution of the equation and a shift in the coordinate origin). As shown above, for the downstream wave the perturbation about
the zero steady state has three real and negative eigenvalues which are considered ‘stable’ since the solution
\[ U \sim U_0 e^{\lambda_1 z} + U_1 e^{\lambda_2 z} + U_2 e^{\lambda_3 z} \]
(where \( U_0, U_1 \) and \( U_2 \) are unknowns) is required to tend to zero as \( z \to \infty \). For the perturbation about the coexistence steady state \( (z \to -\infty) \) there are two negative real eigenvalues (unstable) and one positive real (stable) eigenvalue so that there are 4 stable eigenvalues in total. Thus, the three boundary conditions (4.17) require one further condition to ensure well-posedness. Since the wave solution is invariant to any translation of the origin, it is possible to fix a value for \( U_b \in (0, 1) \) at \( z = 0, U_b = 0.5 \) say, this provides the final boundary condition and it is therefore expected that the problem is well-posed. A similar approach is taken in an example given in [47, page 282].

Upstream

Now consider the wavefront travelling in the upstream direction \((c < 0)\). The characteristic equation for the perturbation about \((0,0,0)\) as \( z \to -\infty \) is given by
\[ P_0^-(\lambda) = \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3, \]  
where the coefficients \( a_i \) are now given by
\[ a_1 = \beta_0 - c, \]
\[ a_2 = 1 - \beta_0 c, \]
\[ a_3 = \mu + \beta_0. \]

Here, since \( z \to -\infty \), stable manifolds correspond to those eigenvalues with positive real parts. Factorising (4.23) and setting it equal to zero yields
\[ (\lambda - s_1)(\lambda - s_2)(\lambda - s_3) = 0, \]
where \( s_i \) are the required eigenvalues. Note that \( a_3 > 0 \Rightarrow -s_1 s_2 s_3 > 0 \Rightarrow s_1 s_2 s_3 < 0 \), so the product of the eigenvalues is negative. There are three possibilities.

- \( s_1, s_2, s_3 < 0 \). For a cubic equation such as (4.23), the Routh-Hurwitz conditions (see [47], A2 1) for \( \text{Re} \lambda < 0 \) are
\[ a_1 > 0, \quad a_3 > 0, \quad a_1 a_2 - a_3 > 0. \]
Suppose \( s_1, s_2, s_3 < 0 \) and assert that \( a_1 > 0 \) (so that \( \beta_0 > c \)), then

\[
\begin{align*}
& a_1 a_2 - a_3 > 0 \Rightarrow (\beta_0 - c)(1 - \beta_0 c) - \beta_0 - \mu > 0 \\
& \Rightarrow -\beta_0^2 c - c + \beta_0 c^2 - \mu > 0 \\
& \Rightarrow -\beta_0 c(\beta_0 - c) - c - \mu > 0
\end{align*}
\]

This is a contradiction since \( \beta_0, \mu > 0 \) and therefore the Routh-Hurwitz conditions cannot all be satisfied. Thus, the case for 3 negative eigenvalues is not possible

- \( s_1 < 0 \) and \( s_2, s_3 > 0 \) This is the only remaining feasible case

So for the upstream wave, there is one negative (unstable) and two positive (stable) eigenvalues for the perturbation about the zero steady state

As described above for the downstream case, solutions of (4.23) are all real only when \( |\Omega|^2 \leq 4a^3 \) Equation (4.21), with \( c < 0 \), may again be used to perform similar analysis to that described above for the downstream case to prove the existence of a minimum wavespeed, \( c_{\text{min}}^- \), such that \( g_u(c) < 0 \) for all \( c \leq c_{\text{min}}^- \), given that

\[
\lim_{c \to -\infty} g_u(c) = -\infty
\]

Figure 4.14 shows equivalent plots to those previously discussed for the downstream case for \( c_{\text{min}}^- \). Qualitatively \( c_{\text{min}}^- \) behaves similarly to \( c_{\text{min}}^+ \) with increasing \( \beta_0 \) and \( \mu \) monotonically decreasing and bounded below by \( c_{\text{min}}^- = 2 \) for increasing \( \beta_0 \) and monotonically increasing for increasing \( \mu \). An unexpected prediction of the model is that the watercourse not only enhances the rate of spread of \( F \) japonica in the downstream direction, but also that in the upstream direction. Although somewhat counterintuitive, this is explained rather simply, the tail of the upstream wave contributes to the waterborne population, some proportion of which will be washed up on the bank before flowing past the advancing wavefront. This augments the population density at that point and promotes the wave’s rate of advance. The effect is clearly strongest for large \( \mu \), reflecting the need for high rates of fragment deposition and regeneration for the effect to be significant.

For the perturbation about the coexistence steady state \((U_b, U_w, W_b) = (1, \frac{1}{\beta_0}, 0)\), the characteristic polynomial (4.22) is obtained. Since \( c < 0 \) for the upstream wave, there are therefore one positive (unstable) and two negative (stable) real eigenvalues. These two stable
Figure 4.14: Implicit solutions of $g(c_{\min}) = 0$. Left: The solutions for $c_{\min}$ on $\beta_0 \in [0.1, 5]$ with $\mu = 0.05, 0.2, 1, 5$ (black, red, green and blue respectively). Right: The solutions for $c_{\min}$ on $\mu \in [0.1, 5]$ with $\beta_0 = 0.05, 0.2, 1, 5$ (black, red, green and blue respectively). Note that $c$ here is the magnitude of $c_{\min}$.
eigenvalues and the two from the perturbation about the zero steady state mean that, as for the downstream case, there are 4 stable eigenvalues in total. By the same reasoning as previously discussed, the problem is therefore expected to be well-posed.

4.6 Simulation of the 1D Riparian Model

The simplified 1D riparian model (4.12) was solved using an explicit finite difference scheme, simulated in Matlab. The code is straightforward and proceeds as follows:

1. Simulation parameters are set. These include $\beta_0$ and $\mu$ (see below for values), the domain size ($K = 10,001$ nodes), spatial step-length ($\Delta x = 0.25$), temporal step-length (e.g. $\Delta t = 0.01$) and the total time to run the simulation for (e.g. $T = 20$). Also set is a threshold value (e.g. $\eta = 0.1$) for which the simulation terminates should the population density on the bank, $b_i$, at the boundaries exceed it (this may occur before the full preset timespan, depending on the resulting wavespeed).

2. Initial conditions are set. The initial bank population, $b^0 = 1$, is set over 100 nodes spanning the centre of the domain. The initial waterborne population is set to $w^0 = 0$ throughout the domain.

3. Markers are created at either side of the initial bank population in order to monitor the spatial position, $x^*$, of where $b = 0.5$ throughout the simulation. $x^*$ is calculated by interpolating between the spatial positions of the nodes at either side of this point. By tracking these markers in time an approximation for the simulated wave-speeds for the upstream and downstream waves can be determined.

4. Solution begins. At each time-step the system is updated according to the following scheme:

$$b_{i+1} = \frac{\Delta t}{\Delta x^2} (b_{i+1} - 2b_i + b_{i-1}) + \Delta t(b_i + \mu w_i)(1 - b_i) + b_i$$

$$w_{i+1} = \frac{\Delta x_i}{2 + \Delta x_i \beta_0} (b_i + b_{i+1} - \beta_0 w_i) + \frac{2w_i}{2 + \Delta x_i \beta_0}$$

(4.24)

where $b^i_t \equiv u_b(x = i\Delta x, t)$ and $w^i_t \equiv u_w(x = i\Delta x, t)$. Here, an explicit finite difference scheme has been implemented for $b_i$ (forward difference in time and central difference in space) and the trapezium method scheme on $w_i$. Due to the terms being linear, $w_{i+1}$ can be found explicitly. As described in Appendix A, it may be shown that the truncation error of the scheme is $O(\Delta x^2 + \Delta t)$.  

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5. In general, the simulation ends at \( t = T \). However, certain parameter values cause the simulated spread to be extremely rapid downstream. As a consequence, the population density may reach significant enough levels \( (b_0, b_K > \eta) \) at a boundary to terminate the simulation prematurely.

### 4.6.1 Results

The programme was used to investigate the effects of varying the parameters \( \beta_0 \) and \( \mu \). Specific values chosen were \( \beta_0 = 0.2, 1, 5 \) and \( \mu = 0.2, 1, 5 \), representing 'small', order 1 and 'large' cases. As an example of the general behaviour of the simulations, Figure 4.15 shows the temporal evolution of the simulated \( u_b \) and \( u_w \) wave profiles for \( \beta_0 = 0.2, \mu = 0.2 \). It is clear to see that the downstream wave travels much more quickly than the upstream one for both \( u_b \) and \( u_w \). Also, as expected the populations behind the wavefronts tend to their predicted nonzero steady states, \( u_b = 1 \) and \( u_w = 1/\beta_0 \) (as detailed in Section 4.5).

![Figure 4.15: Temporal evolution of simulated \( u_b \) (left) and \( u_w \) (right) travelling wave profiles for \( \beta_0 = 0.2 \) and \( \mu = 0.2 \). Initial conditions are shown in blue whilst the profiles at \( t = 4, 8, 12, 16, 20 \) are shown in green, red, cyan, magenta and yellow respectively. Note that the downstream wave (right-moving in this diagram) exhibits much faster spread than the upstream (left-moving) wave.](image)

Table 4.1 shows the minimum wavespeeds predicted by the simulation in the upstream \( (c_{\min}^-) \) and downstream \( (c_{\min}^+) \) directions for various parameter configurations. Also shown for comparison are the analytic wavespeeds calculated by solving (4.21) with \( g = 0 \) in order to find the minimum wavespeed.

Figure 4.16 shows the wavespeed evolutions for the upstream and downstream waves in simulations for \( \beta_0 = 0.2 \) with \( \mu = 0.2 \). After an initially rapid increase the wavespeeds in both directions approach their analytically predicted values (Table 4.1). In fact all wavespeeds
<table>
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<th>Analytic $c_{min}$</th>
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</tbody>
</table>

Table 4.1: Wavespeeds predicted by simulations of the 1D riparian model. †The simulation for $\beta_0 = 0.2, \mu = 5$ results in an extremely fast downstream wavespeed. Here, the simulation was run on a domain of $K = 200,001$ nodes with $\Delta x = 0.05$ and $\Delta t = 0.001$ in order to improve the accuracy of simulation results. The simulation was terminated at $t = 4.182$ due to hardware limitations.

predicted by the simulations agree well with their analytic equivalents, even over the relatively small timespan $T = 20$. It should be noted that it was necessary to reduce the spatial and temporal step lengths ($\Delta x = 0.05$ and $\Delta t = 0.001$) and increase the domain size ($K = 200,001$ nodes) in order to obtain accurate results for the case $\beta_0 = 0.2$ with $\mu = 5$. It is clear to see that the downstream wavespeed in particular is significantly affected by both parameters. For small $\beta_0$, downstream spread is extremely rapid, even when $\mu$ is small relative to $\beta_0$. As $\beta_0$ increases the wavespeed rapidly becomes much smaller in magnitude, even for large $\mu$, although it still exhibits faster spread than the standard Fisher model. The effects of both parameters are similar for the upstream wave, although in this case the magnitude of the wave speed is generally much slower than the downstream wave. For the upstream wave to exhibit a speed significantly greater than that predicted by the Fisher model (as seems to be the case in the observed data from the Swansea surveys), $\mu$ must be considerably larger than $\beta_0$, suggesting that this may be an appropriate parameter regime for the model.
Figure 4.16: The temporal evolution of the magnitudes of the simulated upstream (left) and downstream (right) wavespeeds for $\beta_0 = 0.2, \mu = 0.2$.

Figure 4.17: The global domain was compartmentalised into distinct areas which were subject to different governing equations. Left: A simplified example map (from the Swansea survey data shown in Figure 4.9) converted into 'normal' (green), 'watercourse' (blue), 'bank' (red) and 'inviable' (grey) zones. Right: A zoomed-in area of the map showing the bank nodes between normal and watercourse nodes. The bank nodes are viable for normal growth but, since they are adjacent to the watercourse, are additionally under the influence of the transport of rhizome fragments in the water flow.
4.7 Combining the Fisher Model with the Riparian Model

The Matlab simulation of the Fisher model (discussed in Section 4.3) was extended to incorporate the influence of watercourses in riparian environment. This was achieved by compartmentalising the 2D domain into regions (Figure 4.17) depending on the habitat type and applying the relevant system in each:

1 Normal zones  For the substrate viable for normal growth and where diffusive spread of the aerial stems may be assumed ('normal' zones, Ω), the 2D Fisher equation (4.6) was used as before. Then, nondimensionalising by taking $t' = rt$, $x' = x\sqrt{\frac{r}{D}}$, $y' = y\sqrt{\frac{r}{D}}$ and dropping asterisks for convenience yields

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} + u(1-u)$$

The temporal derivative was approximated by a forward difference representation and the spatial derivatives were again approximated by their central difference equivalents, giving the explicit finite difference scheme

$$u_{i,j}^{t+1} = \Delta t \left( \frac{u_{i,j}^t - 2u_{i,j}^t + u_{i,j+1}^t}{h^2} + \frac{u_{i-1,j}^t - 2u_{i,j}^t + u_{i+1,j}^t}{h^2} \right) + \Delta t u_{i,j}^t (1 - u_{i,j}^t) + u_{i,j}^t$$

2 Watercourse and inviable zones  Watercourses ('watercourse' zones), roads and other obstacles ('inviable' zones) that prohibit the diffusive spread and may be assumed to have a carrying capacity of zero were considered as sterile regions with zero-flux boundary conditions so that the plant could not grow into these areas. At the boundaries, the finite difference molecules were formed in the standard way when using zero-flux boundary conditions as described in Section 4.3.

3 Bank zones  Nodes on the mesh that belonged to the viable growth domain that were adjacent to watercourse nodes were considered as 'bank' nodes, Γ. These form a 1D line of nodes along the bank of the watercourse (see Fig. 4.17). For these nodes, the simplified riparian model (4.12) in 2D was applied instead of the standard Fisher model.
model
\[
\frac{\partial u_b}{\partial t} = \left( \frac{\partial^2 u_b}{\partial x^2} + \frac{\partial^2 u_b}{\partial y^2} \right) + (u_b + \mu u_w)(1 - u_b) \tag{4.25}
\]

\[
\frac{\partial u_w}{\partial \xi} = u_b - \beta_0 u_w
\]

where $\xi(x, y)$ is the bank coordinate along the watercourse, i.e., the spatial arc length distance along the curved bank of the watercourse relative to some origin. This was approximated by the following finite difference scheme

\[
b_{i,j}^{t+1} = \frac{\Delta t}{l^2} (b_{i,j+1}^t - 2b_{i,j}^t + b_{i,j-1}^t) + \frac{\Delta t}{h^2} (b_{i+1,j}^t - 2b_{i,j}^t + b_{i-1,j}^t) + \Delta t (b_{i,j}^t + \mu w_{i,j}^t)(1 - b_{i,j}^t) + b_{i,j}^t \tag{4.26}
\]

\[
w_{k+1} = \frac{\xi_k}{2 + \frac{\xi_k \beta_0}{2}} (b_k + b_{k+1} - \beta_0 w_k) + \frac{2w_k}{2 + \frac{\xi_k \beta_0}{2}}
\]

Here, $b_{i,j}^t$ is the population density on the bank at the gridpoint $(i, j)$ at time-step $t$, $w_{i,j}^t$ is the waterborne population density at the gridpoint $(i, j)$ at time-step $t$, $b_k$ and $w_k$ are their respective equivalents at the $k^{th}$ node along the riverbank and $\xi_k$ is the spatial distance between the $k^{th}$ and $k+1^{th}$ nodes along the bank. In practice, $\xi_k = l, h, \sqrt{l^2 + h^2}$ depending on whether the neighboring node in question is horizontally, vertically or diagonally adjacent respectively. In the first equation, the spatial derivatives are approximated by central differences and the time derivative is approximated by its forward difference equivalent. In the second equation, a forward difference approximation is used for the spatial derivative but the trapezoidal method is again used to represent the right hand side in the second equation of (4.25), thereby increasing the order of accuracy of the approximation to second-order

\[
u_b - \beta_0 u_w \approx \frac{1}{2} (b_{k+1} - \beta_0 w_{k+1} + b_k - \beta_0 w_k)
\]

4.7.1 Stability of the Numerical Solution

For the normal growth and spatial spread on nodes in $\Gamma$, we have the explicit scheme

\[
b_{i,j}^{t+1} = \frac{\Delta t}{l^2} (b_{i,j+1}^t - 2b_{i,j}^t + b_{i,j-1}^t) + \frac{\Delta t}{h^2} (b_{i+1,j}^t - 2b_{i,j}^t + b_{i-1,j}^t) + \Delta t (b_{i,j}^t + \mu w_{i,j}^t)(1 - b_{i,j}^t) + b_{i,j}^t \tag{4.27}
\]
Appendix A demonstrates that (4.27) has a truncatition error

\[ T_{i,j}^t = \frac{\Delta t}{2} \frac{\partial^2 B_{i,j}^t}{\partial t^2} - \frac{\nu^2}{12} \frac{\partial^4 B_{i,j}^t}{\partial x^4} - \frac{h^2}{12} \frac{\partial^4 B_{i,j}^t}{\partial y^4} + O(\Delta t^2) - O(t^4) - O(h^4) \]

that vanishes as \( \Delta t, t, h \to 0 \). Equation (4.27) is therefore consistent with equation (4.25).

Li et al. [44] derive conditions for the convergence and stability of an explicit finite difference scheme for 2D reaction-diffusion equations of the form

\[ \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} + f(u), \]

\[ 0 < t \leq T, \quad (x, y) \in \Omega, \]

\[ u(x, y, 0) = u^0(x, y), \]

\[ u(x, y, t) = 0, \quad (x, y) \in \partial \Omega, \]

where

\[ \Omega = \{(x, y) \mid |x| < a, |y| < b\} \]

and

\[ f(u) \in C^1[0, 1], \]

satisfying

\[ f(0) = f(1) = 0. \]

A similar method to that reported in [44] may be used in this case to show that for the explicit scheme (4.27), convergence and stability are assured for

\[ \Delta t \leq \frac{h^2 \nu^2}{2(l^2 + h^2)} \quad (4.28) \]

4.7.2 Simulation Procedure

The simulation programme is intended for use as a tool for modelling situations observed in the field. As such, the facility to import observed data such as maps and current stand locations in as simple a way as possible has been the subject of much consideration in the design of the programme itself. The resulting automation, image processing and data extraction facilities were discussed for the Fisher model simulation in Section 4.3 and are used again in the code for this simulation programme. The programme proceeds as follows:

1. Simulation parameters are set including
• The geographical map for use as the spatial domain. This may be an arbitrary map, although some pre-processing may be necessary to make it compatible with the programme.

• If GIS or similar data is to be used, a map including an existing stand of *F. japonica* plotted on it may be loaded. This is used later to automatically extract the initial conditions to be used in the simulation.

• Reduction factor. The domain map is automatically reduced in pixel size by some factor. This reduces the final domain mesh so that the simulation has a coarser resolution and fewer gridpoints to update per time-step.

• Time span and temporal interval. The total time over which to run the simulation and the time-step $\Delta t$. $\Delta t$ must satisfy equation (4.28) to ensure stability of the finite difference scheme.

• Spatial settings. $L$ and $H$ are the number of gridpoints in the $x$ and $y$ directions respectively. These are directly determined by the dimensions of the domain map and the reduction factor. It is subject to $l (\equiv \Delta x)$ and $h (\equiv \Delta y)$ are the node separations in the $x$ and $y$ directions respectively.

• Rate of contribution to the bank population from the waterborne population, $\mu$.

• Rate at which waterborne population is washed out of the system, $\beta_0$.

2 Process domains. A number of options are presented via dialogue boxes in order to set up the simulated domains as required. Firstly, domains may be manually defined via use of Matlab’s ‘ginput’ function. The map is displayed as a figure and the user may mouse-click individual points on the map to mark out the domains as required. Alternatively, the map may be automatically processed by the programme. This requires some pre-processing of the map into a useable format with normal zones coloured green, watercourses coloured blue and inviable zones coloured grey. The programme identifies the zones by scanning the colour data and translating it into a code for the relevant domain type. Normal nodes neighbouring watercourse nodes are subsequently converted into bank nodes. Figure 4.17 illustrates an automatically processed map.

3 Define initial conditions. Again, dialogue boxes are used to make choices concerning the setup of initial conditions. Multiple stands of *F. japonica* may be plotted on the map manually using the ‘ginput’ function, returning the coordinates relative to the grid. These are then used to define polygons on the map and any nodes that lie within such polygons are assigned the initial population $u_{0,j} = 1$ in $\Omega$ or $b_{0,j} = 1$ for nodes in $\Gamma$. All other nodes are assigned $u_{0,j}, b_{0,j} = 0$ accordingly.
Alternatively, if the original global domain map has an existing stand of *F. japonica* plotted on it, this stand may be extracted for use as initial conditions automatically as discussed previously in Section 4.3 and depicted in Fig. 4.5

4. Define watercourse flow direction and sort bank nodes accordingly. The map is again displayed as a figure (including the newly-defined initial conditions) and the user is asked to mouse-click close to the point on the bank that is to be considered the ‘source’ (i.e., the bank node that is furthest upstream) of the flow. The programme then finds the address of the bank node closest to the point clicked that lies on the global boundary and considers it to be the furthest upstream bank node. This address is stored as the first element in an array. Next, the bank node adjacent to the first element is found and stored as the next element in the array. This process is iterated until no further bank nodes are found directly adjacent to the last element in the array. The array then defines the addresses, in order, of all bank nodes along one side of the watercourse from source to sink. All remaining bank nodes not in this array are assigned to another array storing the addresses of the opposing bank nodes. At present these play no further part in the simulation and are considered as normal nodes. Thus, the programme is limited to simulating stands on one side of a watercourse only. This is a possible feature for further development in future work. Finally, the distances between neighbouring bank nodes are calculated and stored.

5. Define waterborne population initial conditions. Once the number of bank nodes, $K$, is known, an array of appropriate size is created to store the initial conditions of the waterborne population at each bank node. These are taken to be $w_k = 0$ for $k = 1, 2, \ldots, K$.

6. Set up finite difference molecule. Vectors representing the four directions in the finite difference molecule (see Fig. 4.1) are created. These vectors store addresses that point to nodes in the original domain map. For each node in the global domain, the viable directions for growth are stored in the relevant addressing vectors. Since zero-flux boundary conditions,

$$ \frac{\partial u}{\partial x} \approx \frac{u_{i,j+1} - u_{i,j-1}}{2l} = 0 $$

$$ \frac{\partial u}{\partial y} \approx \frac{u_{i+1,j} - u_{i-1,j}}{2h} = 0, $$

are in effect, it may again be deduced that $u_{i+1,j} = u_{i-1,j}$ or $u_{i,j+1} = u_{i,j-1}$ at the boundary, depending on whether the node is vertically or horizontally adjacent to the
boundary. Thus, nodes at a boundary may have one or more of their finite difference atoms replaced by the relevant substitute. This is the final step in the initialisation of the simulation.

7 Solve At each time-step, the current state of the populations at each node is updated by the relevant scheme, as detailed above, for the different domain types.

4.7.3 Results: Sensitivity Analysis

Initially, it was intended that samples of the Swansea survey data be used for validation of the model output. However, in isolation these are actually unsuitable for such use for number of reasons, the most important being:

1. At present no data were obtainable regarding which stands have undergone any form of management (which can significantly affect spread rates both positively and negatively).

2. The scale of these maps is not clear, making estimation of stand size and area difficult.

3. The stands clearly have many obstacles and external influences affecting the shape of their development, such as roads, watercourses, buildings and walls. Identification of the nature of these on the maps is difficult in some cases.

The work currently underway by CABI Biosciences (see [29]) should produce similar data to the Swansea survey over the next few years but without any of these restrictions, making it potentially much more useful for model validation. In the absence of such data, a parameter survey was carried out in order to investigate the sensitivity of the area expansion over time predicted by the simulations by varying the two main parameters, $\mu$ and $\beta_0$. Simulations were carried out under the following settings and parameters:

- The domain map used was a sketch map of an area of the Nar Valley, Norfolk (Lat. 52 43 03N, Lon 0 23:23E). Figure 4.18 shows this map modified for use in the simulation. The road running North-South is Low Road in Saddle Bow and the river shown is the Nar. This map is used purely for example purposes and because the direction of watercourse flow is known to the author. It is not known whether any $F. japonica$ may be found at this site in the field.

- Initial conditions were input manually, the shape of which was arbitrarily chosen. Identical initial conditions were then used throughout. Figure 4.18 (right) illustrates the particular initial conditions used.
Figure 4.19 shows the evolution of the location of the simulated stand (left) and the bank (centre) and waterborne (right) population wave profiles for \( \beta_0 = 0.2, \mu = 0.2 \) at \( t = 0, 1.95, 3.90, 5.85, 7.81 \). At \( t = 0 \) there is no population either on the bank or in the water since the initial conditions are such that they do not extend on to the bank. At \( t = 1.95 \) the stand has reached the bank of the watercourse and both wave profiles already clearly show an extended wavefront in the downstream direction. By \( t = 3.90 \) the extended front has become much more pronounced and by \( t = 5.85 \) the analytically predicted nonzero steady states are being approached behind the wavefronts. Finally, the simulation is terminated at \( t = 7.81 \) when the simulated bank population exceeds the predefined termination threshold at the boundary.
Figure 4.19: The evolution of the location of the simulated stand (left) and the bank (centre) and waterborne (right) population wave profiles for $\beta_0 = 0.2, \mu = 0.2$. Data shown is for (from top to bottom) $t = 0, 1.95, 3.90, 5.85, 7.81$. 
Figure 4.20 shows the final state of the control simulation ($\beta_0 = 0, \mu = 0$). The simulation has produced, as expected, a single stand expanding away from the watercourse in a roughly circular shape (allowing for distortion due to image processing). The profile of the population density along the bank itself exhibits wavefronts for both the upstream and downstream waves of a typical shape as predicted by the standard Fisher model. The watercourse has no effect on the rate of expansion except as a standard zero-flux boundary. This is reflected by the control simulation taking the longest time to reach the boundary (see Table 4.2).

![Image of Figure 4.20](image)

**Figure 4.20:** The final state of the control simulation ($\beta_0 = 0, \mu = 0$). Left: The simulated stand (purple) superimposed on the domain map. Right: Profile of the population density, $b_{i,j}$, along the bank of the watercourse.

<table>
<thead>
<tr>
<th>$\beta_0$</th>
<th>$\mu$</th>
<th>Time Ended</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>8.98</td>
</tr>
<tr>
<td>0.2</td>
<td>0.2</td>
<td>7.81</td>
</tr>
<tr>
<td>0.2</td>
<td>1</td>
<td>2.72</td>
</tr>
<tr>
<td>0.2</td>
<td>5</td>
<td>0.35</td>
</tr>
<tr>
<td>1</td>
<td>0.2</td>
<td>8.96</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>8.86</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
<td>8.31</td>
</tr>
<tr>
<td>5</td>
<td>0.2</td>
<td>8.97</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>8.94</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
<td>8.75</td>
</tr>
</tbody>
</table>

Table 4.2: Simulation termination times. This is the time-step immediately preceding that at which $b_{i,j} > 0.1$ at one of the boundaries.

Figure 4.21 shows the final state of simulated stands for $\beta_0 = 0.2$ with $\mu = 0.2, 1, 5$. The faster downstream spread for larger $\mu$ predicted by the 1D model (see Table 4.1) is
clearly exhibited here. For $\mu = 0.2$ the downstream spread is relatively slow, meaning a much broader stand may form along the bank prior to the stand reaching the boundary of the domain (thereby terminating the simulation). At the other extreme, $\mu = 5$ results in such rapid spread that both the main stand and the regenerating fragments along the bank have had little time to expand normal to the watercourse. Consequently, a much thinner extension of the main stand stretches out along the bank and the simulation is terminated much sooner than for smaller $\mu$ (see Table 4.2). Note that for $\mu = 1$ and $\mu = 5$, the monotonically decreasing downstream bank population wavefront exhibited by simulations run under other parameter sets is not predicted. Instead, spikes develop early on in the simulation and remain at fixed locations throughout. Initially this was thought perhaps due to the particular approximations used being too crude. However, varying the spatial and temporal step sizes produces repeatable and consistent results. The cause is therefore likely to be something else. The spikes may actually be solutions to the system used after all and their existence may simply be an artifact of the way in which the bank of the watercourse is described as being piecewise continuous. This remains conjecture at present and further work is required to identify their causal factors. However, it is clear that the spikes only seem to appear in the downstream direction when $\mu$ is large relative to $\beta_0$ (similar behaviour, albeit not as extreme, may also be seen in Figure 4.22 for the downstream wavefront for $\beta_0 = 1$ with $\mu = 5$).

Figure 4.22 shows the final state of simulated stands for $\beta_0 = 1$ with $\mu = 0.2, 1, 5$. For $\mu = 0.2$ there is little obvious qualitative difference between this and control simulation. Indeed, Table 4.2 illustrates that there is only a relatively small difference between the times taken for the two simulated stands to reach the boundary. Physically, the majority of plant fragments in the flow are washed out of the system so that few are left to colonise fresh stands, resulting in only a small increase in the spread rate along the bank. For $\mu = 1$ the faster spread is more apparent, showing a larger range attained in a shorter timespan. This is accentuated even further for $\mu = 5$ where the simulation also displays marked qualitative differences. The effects of the faster wavespeeds are clearly visible with the stand expanding particularly rapidly downstream.

Figure 4.23 depicts the final state of simulated stands for $\beta_0 = 5$ with $\mu = 0.2, 1, 5$. There is very little qualitative difference between the shape of the simulated stands for all values of $\mu$ investigated. Indeed, there is little to differentiate between these and the control simulation. However, as expected, the bankside waves are seen to travel with greater speed for higher values of $\mu$ as evident in the simulation termination times in Table 4.2.
Figure 4.21: The final state of the simulations for $\beta_0 = 0.2$ and (top to bottom) $\mu = 0.2, 1, 5$. Left: The simulated stand (purple) superimposed on the domain map. Right: Profile of the population density, $b_{i,j}$, along the bank of the watercourse.
Figure 4.22: The final state of the simulations for $\beta_0 = 1$ and (top to bottom) $\mu = 0.2, 1, 5$. Left: The simulated stand (purple) superimposed on the domain map. Right: Profile of the population density, $b_{i,j}$, along the bank of the watercourse.
Figure 4.23: The final state of the simulations for $\beta_0 = 5$ and (top to bottom) $\mu = 0.2, 1, 5$. Left: The simulated stand (purple) superimposed on the domain map. Right: Profile of the population density, $b_{i,j}$, along the bank of the watercourse.
4.8 Discussion

In this chapter a compartmentalised 2D model for the spatial spread of the aerial stems in *F. japonica* was constructed. This model was formed by combining a 2D Fisher model, used for the spatial spread in 'normal' areas, with a 1D model formulated for application along the banks of a watercourse. The riparian model was constructed by the extension of a standard 1D Fisher model with logistic growth to incorporate terms expressing the effects of a watercourse on the spread of *F. japonica* along its banks. The resulting riparian model was then coupled with the previously mentioned standard 2D Fisher model in a simulation programme. This programme features many advanced facilities including the ability to use a pre-processed arbitrary map. It can then automatically translate the map into various domain types and apply the relevant model in each. In this way the two models are coupled, thereby allowing a more comprehensive model for use on riparian environments. In fact the programme may just as easily be applied for non-riparian habitats, since the riparian component would simply be ignored in this case.

Section 4.2 introduces a simple Fisher model that is used to model the spread of stems on a slightly larger scale than the correlated random walk model. Its use as a phenomenological model is justified by the fact that both the correlated random walk and the Fisher model predict quadratic growth of stand area in time. The model is solved in the simulations by using an explicit finite difference scheme. The advanced features included in this simulation programme, such as the automatic map-processing and custom initial conditions, were further extended for use in the simulation of the riparian model.

Since *F. japonica* is so commonly found in riparian habitats and its rapid spread so well documented (for example, the Swansea surveys show coverage of *F. japonica* along riverbanks increasing from 0.9 ha in 1992 to 5.7 ha in 1998 [19]), the inclusion of the influence of the watercourses in a model is a natural progression from modelling isolated stands. The 1D riparian model extends the Fisher model by adding terms dealing with the loss of plant fragments to and subsequent gain from the flow. The basic model is formulated and simplified, followed by identification and classification of steady states. Travelling wave analysis is then undertaken, resulting in an equation that may be implicitly solved in order to deduce values for the minimum wavespeeds in the upstream and downstream directions. As predicted by both the analysis and the simulation, wavespeeds in both directions are enhanced by the presence of a nearby watercourse. Although the evidence supporting this prediction is abundant for the downstream case, it is not known whether enhanced upstream spread is borne out in the field. It is expected that such an effect would be negligible in the field due to the key causal factor in the models being the long tail of the upstream
wavefront, something that does not exist in the field. However, some of the Swansea data does seem to support the prediction of faster upstream spread, but in these cases it is not clear what barriers to growth and management the stands have been subject to. According to the predictions of the model, one possible explanation for such behaviour in the field might be that the fragments exhibit a high viability for regeneration (equivalent to large \( \mu \)). The prediction presents an interesting area of study for field investigations.

As with the correlated random walk model discussed in Chapter 3, a lack of field data currently inhibits parameterisation and validation of the model predictions. However, since the model is used on a purely phenomenological basis and has so few parameters controlling it, this should be a task that is somewhat smaller in magnitude. Here, only spread rate data is required. Given empirical data on the rates of advance of \( F. japonica \) both upstream and downstream, appropriate values of \( \beta_0 \) and \( \mu \) may be extracted from the results presented in this chapter. Let \( c_f \) be the minimum wavespeed predicted by the Fisher model, \( c_u \) and \( c_d \) respectively be empirically determined upstream and downstream spread rates and let \( c_n \) be the empirically determined non-riparian spread rate. Then, the ratios

\[
\frac{c_{mn}^+}{c_f} = \frac{c_d}{c_n} \Rightarrow c_{mn}^+ = 2 \frac{c_d}{c_n} \\
\frac{c_{mn}^-}{c_f} = \frac{c_u}{c_n} \Rightarrow c_{mn}^- = 2 \frac{c_u}{c_n}
\]

may be used to find realistic values for the nondimensional \( c_{mn}^+ \) and \( c_{mn}^- \). These may then be used to find appropriate values for \( \beta_0 \) and \( \mu \). Since \( \beta_0 \propto \frac{1}{\psi} \) and \( \mu \propto \frac{1}{\psi} \), predictions may be made for other watercourses exhibiting different rates of flow.
Chapter 5

Conclusions and Further Work

But it's not just learning things that's important. It's learning what to do with what you learn and learning why you learn things at all that matters.

_Norton Juster, The Phantom Tollbooth_

This report focuses on the formulation and simulation of stochastic and deterministic mathematical models for the spatial spread of _F. japonica_ in the United Kingdom. Fieldwork was carried out in order to investigate the various morphological properties of the rhizome network and some surface measurements were also taken. The resulting data was analysed and used to parameterise the models and, where possible, validate their predictions. The models themselves consist of a 3D correlated random walk model for the development of the subterranean rhizome network (the plant's primary mode of spread in the absence of disturbance) and a 2D reaction-diffusion model for the spatial spread of the aerial stems, incorporating a compartmentalised 1D model featuring a Fisher-type model for the growth and spread of aerial stems along a river bank coupled with advective dispersal of rhizome and stem fragments in the watercourse. This work was primarily motivated by the need to demonstrate to landowners, developers and funding bodies the need to eradicate the plant on the land they are responsible for as soon as possible. The economic and ecological impacts of the presence of _F. japonica_ are well known, yet it remains notoriously difficult to obtain funding for, or to persuade the parties responsible to, impose management upon the invasive alien plant. The aim of this work was to produce tools that might be used to illustrate graphically and quantitatively the implications of delay when dealing with an infested site, thereby motivating prompt and proper action.

Chapter 1 discusses the background and motivation for the modelling work contained herein. This includes an introduction to the plant itself, its history and uses, its taxonomy, physiology and its morphology. Motivation for the mathematical modelling is discussed by
first examining some of the problems that an infestation of \textit{F japonica} can cause (emphasising both the ecological and economic costs this can present) and some of the management techniques that are currently used to control infestations. Then, a need for a predictive tool for use in promoting the problem, prioritising sites for treatment and cost-effect appraisal of management techniques is established. Existing literature is examined and it was found that, although some modelling of spatial spread in \textit{F japonica} has been attempted previously, none of the existing models were both directed at the required scale (a single clone or local habitat scale) and applicable to the UK problem. The development of an extensive rhizome network beneath the substrate is identified as being the plant’s primary mode of spread in the UK. However, a lack of available data on rhizome network morphology and physiology for use in the parameterisation and validation of the models motivated fieldwork in order to obtain the requisite information.

Chapter 2 identifies the need for a thorough understanding of the subject system prior to any modelling. The lack of data on rhizome network form and function motivates the fieldwork that is discussed in this chapter. The first survey described involved the extraction of rhizome network samples from the periphery of a stand in Cornwall, UK. The site itself is detailed, followed by the methodology and results of some preliminary surface measurements and the subsequent rhizome network measurements. Basic statistical analyses are undertaken and some conclusions about the way in which the rhizome network develops are drawn based on survey observations. Comparisons between the data from this survey and the equivalents from the work of Adachi et al. [3] suggest that the two datasets are statistically different. This may be due to contrasting geographical or climatic features, but is more likely due to the Japanese data actually being based on the dwarf variety, \textit{F japonica} var. \textit{compacta}. The possible existence of a relationship between the age, number of concentric rings and diameter of rhizomes was found. Such a relationship would be extremely useful for determining the age of existing stands, but further investigation is required before any conclusion may be made.

The second survey discussed in Chapter 2 investigates the crown density and growth rate of rhizomes, both of which are important for the modelling. This site showed some evidence of management but efforts were made to take samples from as far away as possible from the affected area. New rhizome growth was readily identifiable and analysis of the resulting data suggested that rhizomes exhibit no longitudinal extension behind the apex once the tougher overwintering state has been formed. Measurement of the crown density provided a useful benchmark for the validation of model output.

The fieldwork was very successful in providing data for use in the modelling and furthering the understanding of rhizome network development. Seven of the thirteen parameters in the
correlated random walk model (see Chapter 3) were assigned values obtained directly from this work. Additionally, various data obtained could be used for model validation. A number of suggestions are made for further investigations to complement the findings from these two surveys.

Chapter 3 presents a stochastic model for the development of a rhizome network. This is approached via the use of a correlated random walk for the rhizome growth, with probability distributions drawn from the field data controlling various aspects of the development such as branching and crown formation. Though somewhat phenomenological in nature, this model uses a large amount of field data in its parameterisation and consequently predicts such data as was available for model validation well. An overview of the model is followed by an account of the model simulation programme. Many simulations were carried out under a standard parameter set (predominantly determined by empirical observations and measurements) and the general behaviour of the model under such conditions was analysed in terms of area expansion rates and predicted crown densities. It was found that the area tends to grow quadratically in time so that \( A(t) \sim A_0 + \alpha t^2 \) where \( A(t) \) is the area of the stand at a time \( t \) years in the future, \( A_0 \) is the initial area and \( \alpha \) is a constant expansion rate determined by simulation. Thus, for large time \( A \sim \alpha t^2 \). No data were available with which to confirm or refute this prediction, presenting an interesting area for further investigation. However, if validated through further fieldwork this represents a very simple and useful formula for application in prioritising sites for treatment. Additionally, it could be used to predict the cost of removal of a stand from a site (see Section 3.5 and below) or to estimate biomass for use in gauging the correct levels of herbicide to use at specific sites.

Of the 13 parameters in the correlated random walk model, 7 parameter values were directly obtained from the field data and another 3 were derived from previous publications. This left only 3 parameters for which no value could be accurately estimated or measured. Thus, parameter surveys were undertaken to investigate the effects of each on the general model output so that suitable values could be assigned to them based on the properties of the simulated rhizome network they predict. A preliminary investigation of the effects of the known parameters was also undertaken, although more work is required here to make any firm conclusions.

The simulation predictions for the increase in stand area over time governed by the standard parameter set were used in a case study illustrating one of the potential practical applications of the modelling. A problem stand in Cornwall (UK) was used as the basis for the prediction of future disposal costs for the management method of extraction of contaminated soil and its subsequent burial at a specialist site. Generally, site-specific data was used to calculate the approximate cost of such an operation for a given volume/mass of contaminated
soil. This information was then coupled with the model's predictions for stand area increase to allow a minimum and maximum estimate of how the disposal costs might increase over time if the stand is left to grow unchecked. The predicted increase in economic costs over the relatively small timescale of 10 years is extremely significant. This represents a powerful motivating factor for dealing with an infestation of *F. japonica* in a timely fashion.

Chapter 4 builds on the results of the study on the correlated random walk to formulate a model for the spatial spread of the aerial shoots of a stand of *F. japonica* at a slightly larger scale, for example greater than 200 m². At such scales the correlated random walk model becomes too computationally intensive, motivating the alternative approach of using a 2D Fisher model which predicts quadratic expansion of area in time in agreement with the correlated random walk model's prediction. The basic model is discussed along with justification for its use in this case. The model is then solved via the use of a finite difference scheme in a Matlab simulation. The advanced features of the programme are discussed, such as manually-definable domains and initial conditions, automatic map-processing and so on.

The basic Fisher model was then used as the basis for a more complex model for the spatial spread of the aerial stems in riparian environments as it is the simplest model that has the property of area expansion being quadratic in time. This problem is demonstrated by examination of GIS data and the regenerative properties of rhizome and stem fragments, thereby motivating the 1D riparian model that is subsequently described. The model consists of the basic Fisher equation in 2D, extended to include terms for the loss of fragments to the watercourse and their subsequent washing up and regeneration into fresh clones. Their transport downstream is handled in an additional coupled equation via simple advection. The model equations are formulated and the boundary and initial conditions stated. Simplification of the model is then undertaken via nondimensionalisation and the assumption that the velocity of flow is large relative to the diffusive spread. The expected large time behaviour of the model is investigated using travelling wave analysis in which an equation for the predicted minimum invasion wavespeed, *cₘₙ*, is derived for both the upstream and downstream cases. It was found that the model predicts not only faster spread in the downstream direction, but the upstream wavespeed can also be enhanced noticeably, albeit to a lesser extent. As expected, these effects were most significant for *β*₂ < 1 with *μ* ≥ *O*(1).

The programme simulating the riparian model is then described. This uses the code for the Fisher model simulations as a base but features a number of enhancements and revisions. The global domain simulated is split into regions depending on the habitat type. In each region the relevant model is applied so that the 2D Fisher model is applied in general viable regions, the 1D riparian model is applied along the bank of the watercourse and inviable regions define zero-flux boundaries. Again, an explicit finite difference scheme
is used to solve the PDEs. Stability conditions for the numerical solution are determined, limiting the size of the temporal step in relation to the spatial step sizes. This is needed to ensure that errors in the simulation do not grow unboundedly. The simulation procedure is then described in detail and the sensitivity of the simulation output to changes in the key parameters $\mu$ and $\beta_0$ is investigated. In all cases with $\mu > 0$ it was found that the speeds of both the upstream and downstream waves along the bank of the watercourse were enhanced relative to the standard Fisher model predictions. As expected, the fastest spread rates were exhibited when $\mu$ was large relative to $\beta_0$ since this combines fewer waterborne fragments being lost to the system with a higher rate of subsequent colonisation, which is in agreement with the analysis. For such simulations, the downstream wavefronts along the bank of the watercourse exhibit somewhat spiky profiles. This phenomenon remains unexplained and presents a possible issue for further investigation.

In general, the incorporation of the 1D riparian model into the original simulation programme has resulted in the creation of a flexible and versatile tool that predicts qualitatively what might be expected to be observed in the field. The collection of relevant field data should allow appropriate parameters to be determined for the model such that an evaluation of its efficacy may be undertaken in the future.

The work presented in this study provides numerous opportunities for extension and further work, some examples of which are discussed below. These may be broadly broken down into two themes: further fieldwork and model development.

Motivation for further fieldwork originates from a variety of sources. These include the following, some of which are discussed in more detail in Section 2.4.

- The first survey extracted rhizomes from only the top 50 cm of soil. Although none were found to grow below this from the subject area on the periphery of the main stand (i.e., those depicted in Figure 2.5), it is possible that rhizomes from the main stand may have extended into the subject area at greater depths. Thus, unearthing of greater depths presents one area for further investigation.

- The subject area in the first survey was on the periphery of the main stand. Rhizomes may have different morphological properties and functional roles in different areas of a stand. Certainly, it is known that rhizomes and crowns can grow much larger than those observed in this survey. It would be interesting to compare the data from this survey with samples from the central part of a stand.

- Whilst as many data as possible were obtained in the two surveys, each represents only a single sample site. Equivalent data from additional sites in similar habitat types are highly desirable.
As well as an increase in the number of sample sites, samples from stands in differing habitat types and environmental conditions would allow not only comparison with data from this study, but also allow the tools described in this report to be used for stands in such environments with a greater degree of confidence in their predictions. As reported in Cain [13] for *Solidago altissima*, different sample sites exhibit a wide variation in the clonal growth parameters. Similarly, *F. japonica* is likely to exhibit such behaviour, suggesting that data from different habitat types might contrast significantly with those from this study. An illustration of the effects of different environmental conditions may be found on drier sites, in which *F. japonica* is known to produce shorter stems and smaller leaves, whilst in shady areas it tends to be more leafy and compact [6]. It is possible that the rhizome network is also affected by such conditions.

The manner in which rhizomes appear to extend at the apex, form nodes and exhibit no further extension behind the apex requires a detailed, targeted study in order to confirm this assertion.

The possible relationship between the age, diameter and number of concentric rings exhibited in rhizome cross-sections would be an extremely useful way to age stands in the field. This is of interest to a wide variety of parties, but would also be useful for the validation of model predictions and provide an alternative method of measuring spread rates.

Since the rhizome growth rate is such an important parameter in the correlated random walk model and in the spread rate of rhizome networks in the field, a more extensive study of this property is highly desirable.

Equivalent field data from both closely-related species and entirely different ones exhibiting similar properties for *F. japonica* would present interesting cases for comparison and contrast.

For the riparian model discussed in Chapter 4, suitable empirically-obtained parameter values are not currently available. Field data on such events as the rate at which fragments of stem and rhizome fall (or are washed) into a watercourse, their transport rates, typical distances they may travel and the rate at which they are washed up again would all aid the correct parameterisation of this model, at least for specific sites.

As discussed in Section 2.2.3, further data on the relationship between primary segment lengths and the higher branching orders is required to confirm the apparent relationship between branching order and segment length.
Opportunities for further development of the simulations as tools and of the underlying models are also wide in scope

- In the correlated random walk model the number of rhizomes generated by newly-formed crowns could be drawn from an empirically-determined probability distribution each time. This is not included in the model at present due to insufficient data.

- Also in the correlated random walk model it is possible to add variable growth rates for the rhizome extension. This could be driven by coupling it with the influence of environmental and seasonal factors as mentioned above.

- The simulation of the correlated random walk model could be extended to automatically provide estimates of subterranean biomass, given the relevant field data.

- Minor modifications to the correlated random walk programme code would allow it to account for the topology of the local environment, such as hills and slopes, by utilising a spatially dependent $h_{\text{min}}$.

- Due to the limitations imposed by available computing resources, detailed investigation of the effects of the known parameter values on simulation output for the correlated random walk model had to be foregone. Preliminary observations suggest that there may be some interesting relationships between these parameter values and the morphology of simulated stands. Parameter surveys akin to those undertaken on the unknown parameters may, therefore, yield results of equal interest. It is possible that some of these relationships may be exploitable in the management of F. japonica.

- It is thought that apical dominance is the main regulatory mechanism for rhizome branching and shoot formation (and, hence, the generation of crowns). The addition of hormonal control of these events in the correlated random walk model, replacing the phenomenological branching trigger lengths and probability of crown generation, would increase the biological accuracy of the model. This would also require the collection of applicable field data.

- Applying the work in this report on a larger scale (for example that of a town or county) may require a fresh approach to the modelling. In particular, long distance dispersal events may become much more important at such scales. Long distance dispersal mechanisms include the transport of rhizome/stem fragments along watercourses (as discussed in Chapter 4), but more often past long-distance dispersal events have been linked to human activity such as fly-tipping, careless management, disturbance by
vehicles along roads and railways, the transport soil contaminated with *F. japonica* rhizome and even direct sales from garden centres. Clearly such events may exhibit a large amount of stochasticity in their frequency and magnitude, something that larger-scale models will need to address.

Additionally, as discussed in Section 3.6, short-range dispersal by disturbance also seems to be an important mechanism for increasing the spread rate of the plant. The inclusion of stochastic short-range fragment dispersal in the models would also make an interesting advancement to this study.

- At present the riparian model assumes that the watercourse is uniformly likely to deposit floating plant fragments at every point downstream along the bank and models two-dimensional diffusion and mixing on the surface of the water by simple wash-out and return functions. However, in the field watercourses may have particular geographical features or flows that result in segments of the bank being more (or less) susceptible to fragments being washed up. More detailed modelling of the flow may identify such sections of the bank.

- Given the relevant data, it would be extremely interesting to model the effects of feedback from environmental conditions, including substrate properties, light availability, competition, altitude and climate. Seasonal fluctuations also play a major role in the plant's life history.

- Incorporation of the application of various management techniques into the models represents perhaps the most practically useful area for further development. In particular, long-term herbicide treatments are a popular method of controlling the plant. The effects of such treatments on the development of the rhizome networks could be used to predict the future costs of management via herbicide. Another, very different, management technique currently being considered is the use of a monophagous predator in a biocontrol programme. A study on the possible impact of such a programme could be achieved by modifying the correlated random walk model.

- The addition of a more aesthetic and ergonomic graphical user interface (GUI) for the simulations would make any distribution and third party use of the Matlab code easier.

The work detailed in this report has elucidated many aspects of the invasive weed *F. japonica*, from morphological and physiological properties to rates and patterns of spread. Much of the resulting field data was previously unknown and there are also many examples which support existing data or present interesting comparisons and contrasts between,
example, closely related species or different habitats. The use of the resulting field data in constructing the mathematical models has enabled the production of simulation programmes that could be extremely useful for application in commercial and conservation settings. However, despite the wealth of new information and potential applications for the models, this study has also generated many new questions and opportunities for further work. It is therefore hoped that it will serve both as a reference text and as an inspiration for further research into the rapid spatial spread of *F. japonica* that has seen the plant increasingly become a persistent and costly problem throughout the British Isles and the rest of its introduced range.
Appendix A

Consistency of the Numerical Solution for the Growth and Spread of \textit{F. japonica} on the Banks of the Watercourse

For the internal points in $\Omega$, the analysis below holds with $w_{i,j}^t = 0$. Let $B(x,y,t) \equiv u_b(x,y,t)$ be the true solution to the first equation in (4.25) and let $T_{i,j}^t$ be the local discretization error (i.e., how well $B_{i,j}^t$ satisfies (4.27)). Then,

$$
T_{i,j}^t = \frac{B_{i,j}^{t+1} - B_{i,j}^t}{\Delta t} - \frac{B_{i,j-1}^{t} - 2B_{i,j}^{t} + B_{i,j+1}^{t}}{l^2} - \frac{B_{i-1,j}^{t} - 2B_{i,j}^{t} + B_{i+1,j}^{t}}{h^2}
$$

so that

$$
B_{i,j}^{t+1} = \Delta t \left( \frac{B_{i,j-1}^{t} - 2B_{i,j}^{t} + B_{i,j+1}^{t}}{l^2} + \frac{B_{i-1,j}^{t} - 2B_{i,j}^{t} + B_{i+1,j}^{t}}{h^2} \right) + \Delta t(B_{i,j}^{t} + \mu w_{i,j}^{t})(1 - B_{i,j}^{t}) + \Delta t T_{i,j}^t + B_{i,j}^{t+1}
$$

Assuming that the true solution $B$ is known at all points up to and including time-step $t$, $b_{i,j}^{t+1}$ represents a local approximation to $B_{i,j}^{t+1}$ where

$$
b_{i,j}^{t+1} = \Delta t \left( \frac{B_{i,j-1}^{t} - 2B_{i,j}^{t} + B_{i,j+1}^{t}}{l^2} + \frac{B_{i-1,j}^{t} - 2B_{i,j}^{t} + B_{i+1,j}^{t}}{h^2} \right) + \Delta t(B_{i,j}^{t} + \mu w_{i,j}^{t})(1 - B_{i,j}^{t}) + B_{i,j}^{t+1}
$$
Subtracting (A 3) from (A 2) yields

\[ B_{i,j}^{t+1} - b_{i,j}^{t+1} = \Delta t T_{i,j}^t, \]

illustrating that \( T_{i,j}^t \) is a measure of the local discretization error for a single application of the finite difference scheme. The order of the local discretization error is determined by writing (A 1) in terms of Taylor series, so that by Taylor's theorem

\[ B_{i,j}^{t+1} = B_{i,j}^t + \Delta t \frac{\partial B_{i,j}^t}{\partial t} + \Delta t^2 \frac{\partial^2 B_{i,j}^t}{\partial t^2} + O(\Delta t^3), \]

giving

\[ B_{i,j}^{t+1} - B_{i,j}^t = \frac{\Delta t}{2} \frac{\partial B_{i,j}^t}{\partial t} + \frac{\Delta t^2}{2!} \frac{\partial^2 B_{i,j}^t}{\partial t^2} + O(\Delta t^3) \]

Taylor's theorem also yields

\[
\begin{align*}
B_{i,j+1}^t &= B_{i,j}^t - t \frac{\partial B_{i,j}^t}{\partial x} + \frac{t^2}{2!} \frac{\partial^2 B_{i,j}^t}{\partial x^2} - \frac{t^3}{3!} \frac{\partial^3 B_{i,j}^t}{\partial x^3} + O(t^4), \\
B_{i+1,j}^t &= B_{i,j}^t + h \frac{\partial B_{i,j}^t}{\partial y} + \frac{h^2}{2!} \frac{\partial^2 B_{i,j}^t}{\partial y^2} + \frac{h^3}{3!} \frac{\partial^3 B_{i,j}^t}{\partial y^3} + O(h^4), \\
B_{i-1,j}^t &= B_{i,j}^t + h \frac{\partial B_{i,j}^t}{\partial y} + \frac{h^2}{2!} \frac{\partial^2 B_{i,j}^t}{\partial y^2} + \frac{h^3}{3!} \frac{\partial^3 B_{i,j}^t}{\partial y^3} + O(h^4), \\
B_{i,j+1}^t &= B_{i,j}^t + h \frac{\partial B_{i,j}^t}{\partial y} + \frac{h^2}{2!} \frac{\partial^2 B_{i,j}^t}{\partial y^2} + \frac{h^3}{3!} \frac{\partial^3 B_{i,j}^t}{\partial y^3} + O(h^4) \\
B_{i,j-1}^t &= B_{i,j}^t + h \frac{\partial B_{i,j}^t}{\partial y} + \frac{h^2}{2!} \frac{\partial^2 B_{i,j}^t}{\partial y^2} + \frac{h^3}{3!} \frac{\partial^3 B_{i,j}^t}{\partial y^3} + O(h^4).
\end{align*}
\]

Thus,

\[ B_{i,j-1}^t - 2B_{i,j}^t + B_{i,j+1}^t = t^2 \frac{\partial^2 B_{i,j}^t}{\partial x^2} + \frac{t^4}{12} \frac{\partial^4 B_{i,j}^t}{\partial x^4} + O(t^5) \]

and

\[ B_{i-1,j}^t - 2B_{i,j}^t + B_{i+1,j}^t = h^2 \frac{\partial^2 B_{i,j}^t}{\partial y^2} + \frac{h^4}{12} \frac{\partial^4 B_{i,j}^t}{\partial y^4} + O(h^5) \]

so that

\[
\begin{align*}
T_{i,j} = \frac{\partial B_{i,j}^t}{\partial t} + \frac{\Delta t}{2} \frac{\partial^2 B_{i,j}^t}{\partial t^2} + O(\Delta t^2) - \frac{\Delta t^2}{2} \frac{\partial^2 B_{i,j}^t}{\partial t^2} - \frac{t^2}{12} \frac{\partial^4 B_{i,j}^t}{\partial x^4} - O(t^4) \\
- \frac{\partial^2 B_{i,j}^t}{\partial y^2} + \frac{h^2}{12} \frac{\partial^4 B_{i,j}^t}{\partial y^4} + O(h^4) - (B_{i,j} + \mu \omega_{i,j})(1 - B_{i,j})
\end{align*}
\]

However,

\[ \frac{\partial B_{i,j}^t}{\partial t} = \frac{\partial^2 B_{i,j}^t}{\partial x^2} + \frac{\partial^2 B_{i,j}^t}{\partial y^2} + (B_{i,j} + \mu \omega_{i,j})(1 - B_{i,j}), \]
meaning
\[ T_{i,j}^t = \frac{\Delta t}{2} \frac{\partial^2 B_{i,j}^t}{\partial t^2} - \frac{l^2}{12} \frac{\partial^4 B_{i,j}^t}{\partial x^4} - \frac{h^2}{12} \frac{\partial^4 B_{i,j}^t}{\partial y^4} + O(\Delta t^2) - O(l^4) - O(h^4). \]

The truncation error \( T_{i,j}^t \) is thus
\[ T_{i,j}^t = O(\Delta t) + O(\Delta l^2) + O(h^2), \]

which is first-order in time and second-order in space. Clearly, \( T_{i,j}^t \to 0 \) as \( \Delta t, l, h \to 0 \) Thus, the difference equation (4.27) is consistent with (4.25)
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