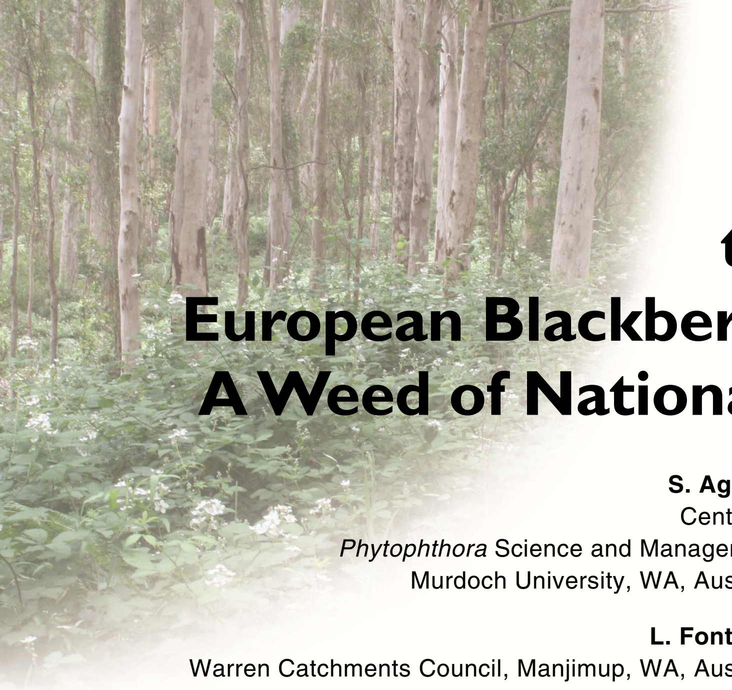

A Conceptual Model to Describe the Decline of European Blackberry (*Rubus anglocandicans*), A Weed of National Significance in Australia

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Human activities have had an adverse impact on ecosystems on a global scale and have caused an unprecedented redispersal of organisms, with both plants and pathogens moving from their regions of origin to other parts of the world (3,8,27,49). Invasive plants are a potential threat to ecosystems globally, and their management costs tens of billions of dollars per annum (14).

Rubus anglocandicans A. Newton (European blackberry, previously included in the aggregate taxon *Rubus fruticosus* L. aggregate) is a serious invasive species in Australia (4). It is one of the original 20 "Weeds of National Significance" and a major weed of conservation, forestry, and agriculture, particularly in wetter regions (50). Herbicide and cultural control methods are generally inefficient or require multiple applications (4,10). Therefore, a biological control program using stem and leaf rust strains is the main option in Australia (6,23,54). However, biological control using rusts has been patchy, as host factors, climate, and weather can alter the impact of the rust at different locations (20,22,47,52). In 2007, Yeoh and Fontanini noticed that blackberry plants (*R. anglocandicans*) on the banks of the Donnelly and Warren rivers in the southwest of Western Australia (SWWA) were dying in areas that were being regularly monitored for the impact of rust as a biological control agent. The symptoms on blackberry became known as the disease "blackberry decline".

The epithets "dieback" or "decline" have been given to many perennial plant diseases to describe either the most significant criterion or the common nature of the specific disease syndrome, and in most cases, the causes are unknown or incompletely understood (34, [but see Ostry et al. (51) for a contrary view]). Therefore, continuous and intensive investigations are required to discover the different biotic and abiotic components associated with specific declines in plant populations. There are numerous examples of decline phenomena in natural ecosystems (18,43,44), including the determination of possible causes through classical and molecular pathology and ecological studies. This has led to the development of specific models for each decline phenomenon. For instance, Flory and Clay (26) hypothesize the ecological consequences of pathogen accumulation for introduced hosts and encapsulate this in the Pathogen Accumulation and Invasive Decline (PAID) model. Elmer et al. (18) have shown the involvement of biotic stressors (*Fusarium* species, nematodes, and herbivores) and abiotic factors such as cyclic drought and rise of the sea level in the sudden vegetation dieback in Atlantic and Gulf Coast salt marshes.

Blackberries are generally more resistant to plant diseases than other *Rubus* species (17). A dieback disease of blackberries affecting primarily the Boysen and Young trailing blackberries was prevalent in nearly all berry growing regions of California during the winters of 1947 to 1948 and 1948 to 1949, but the cause(s) remained unclear (64). Wall and Shamoun (60) investigated diseases of *Rubus parviflorus* (thimbleberry) in British Columbia and cited the association of *Cylindrocarpon destructans*, *Naematoloma fasciculare*, *Resinicium bicolour*, and a *Verticillium* sp. with root rots. Also, a blackberry root rot by *Rhizoctonia solani* has been reported by Cedeño et al. (13). The association of *Cylindrocarpon destructans* var. *destructans* and *Neonectria discophora* var. *rubi* with black foot rot on blackberry (*Rubus glaucus*) has been reported from Merida, Venezuela by Cedeño et al. (12). Hence, based on the literature, there are only a few records of root pathogens involved in blackberry diseases across the world. This paper describes blackberry decline and disease symptoms, epidemiology, and distribution in SWWA. We also present an illustrative model to explain the presence of the disease on blackberry.

Blackberry as a Weed in Western Australia

Blackberries were probably introduced to SWWA soon after European settlement in 1829. At least three species of weedy *Rubus* (blackberry) have established: *R. anglocandicans* (the most widespread species), *R. laudatus,* and *R. ulmifolius* (24). In addition, the cultivated species *R. loganobaccus* (loganberry) and an unidentified blackberry are locally established (24,65).

Blackberry is now widespread in SWWA in areas with more than 800 mm of rainfall per year, with the impact being along watercourses (30). *R. anglocandicans* infestation can reduce plant species diversity by 50% (65). The most important recreational river fishing is for marron (a species of freshwater crayfish, *Cherax cainii*), and the dense thickets of blackberry prevent access to the river banks. In agricultural and forestry situations, *R. anglocandicans* is occasionally a major weed. Commercial production of

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http://dx.doi.org/10.1094/PDIS-11-13-1124-FE

weedy varieties of blackberries is prohibited under state laws (65), and the only positive impact, wild fruit collection, is a minor activity.

Control by herbicides is effective but is limited to accessible areas and requires regular reapplication. Therefore, biological control has been identified as the main strategy for control of blackberry.

Blackberry Biological Control

The only agent so far introduced to Australia for the biological control of blackberry is the rust *Phragmidium violaceum* (Schultz) G. Winter (47). An unknown strain of this rust was found to be widespread in Victoria in 1984 (40). This is referred to as the illegal strain because there was neither prior host-specificity testing of this strain nor any official sanctioning of its release.

Another strain of this rust (F15) was selected for its virulence and reproductive fitness under laboratory conditions, and intentional release was approved officially in 1991 (9). However, Evans et al. (21), using specific molecular markers, showed that the F15 strain did not become well established, as the illegal strain predominated in nearly all populations examined.

In an attempt to find more virulent and better-adapted rust strains capable of affecting Australian blackberry species growing under field conditions, trap gardens with blackberry plants transplanted from Australia were established at Montpellier, France (48). Eight potential effective new strains were identified. These were approved for release in Australia in 2004, with releases of these strains together with F15 beginning in the same year.

In Western Australia, the nine strains of rust were released in autumn and spring 2004 in the Manjimup region (46). As part of a one-year study to gather baseline data on the blackberry infestations within these areas, and to investigate the possibility of integrating chemical and biological control methods, releases of the nine rust strains were made at six sites in the Warren River Catchment and two sites in the Blackwood River Catchment (situated immediately north of the Donnelly River Catchment) during the spring of 2005 (65).

Eight sites used for experiments on treatments with fungicide and/or rust in 2004 and 2005 consisted of dense stands of healthy *R. anglocandicans*. In 2005, sites had on average 9 canes/m^2 or 5.4 plants/m^2 (65). Healthy control plants not inoculated with the rust or sprayed with herbicide were approximately 12 m long, with 95 fruits and 1,800 seeds by the end of autumn (April). In spring 2006, a subset of the eight experimental sites from 2005 was used to set up new experiments designed to measure the impact of the blackberry rust. As part of this study, the fungicide 4Farmers Tebuconazole 430 (active ingredient 439 g/liter tebuconazole) was applied to half the plots (including eight plots, 3 × 2 m) in 2006 onward to control rust (a single application in October 2006 at the future Warren River decline site, followed by monthly applications October 2007 onward).

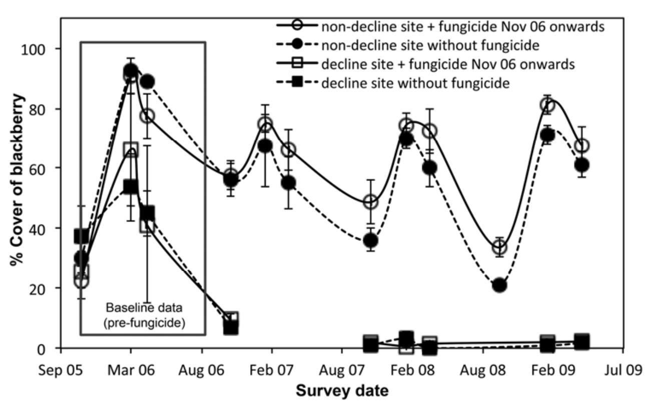

Fig. 1. Seasonal changes in coverage of blackberry (Mean % cover [±SE] [*n* = 4 plots/site]) in a nondecline site and decline site (both on the Warren River, WA). Half the plots at the decline sites were treated with the fungicide tebuconazole from October 2006 to April 2009 (gap shows decline sites not monitored between November 2006 and 2007).

Description of the Study Area: Donnelly and Warren Catchments

The Donnelly and Warren Catchments are 1,688 km^2 and 4,315 km^2, respectively, and located in SWWA. This region has a strongly seasonal humid Mediterranean climate, with most of the rain falling in winter (June to August), and summer (December to February) being dry and hot. Most of the two catchments are covered with *Eucalyptus* forests of karri (*Eucalyptus diversicolor*) or mixed jarrah (*E. marginata*) and marri (*Corymbia calophylla*), with the remainder being farmland. The main towns in the two catchments are Manjimup and Pemberton, and the main industries are farming (started in the 1850s), horticulture, vineyards, timber, and tourism.

Initial Detection of Decline

In November 2006, at the Warren River "decline site", canes throughout the site looked normal but not particularly healthy, and cane densities had fallen to 73% overall in the previous year. Cane densities at the three control healthy sites on the same river were approximately the same as in the previous season (Fig. 1).

Being a semi-deciduous plant, foliage cover varies throughout the year, with a higher level of cover in summer (December to February) than in winter (June to August). In our study area, new-season foliage was produced in October (spring) each year. In November 2006, plants in the decline sites only had 10% of the foliage cover seen the previous year, in contrast to the healthy sites that at the same time had over 60% of their previous year foliage levels (Fig. 2A).

Fig. 2. Blackberry at the Collins Road site, Warren River, WA. **A,** Extensive healthy blackberry in November 2005; **B,** typical blackberry decline, with dead canes on the ground in August 2008 after winter floods.

In October 2007, the blackberry population at the decline sites had crashed, as evidenced by a profusion of dead canes. The damage was more severe and rapid than anything previously observed even after inoculations of *P. violaceum* under laboratory conditions (20). The few new primocanes produced at the decline sites in the following season were thin and weak, and the surviving floricanes failed to produce fruit. Dead stems fell to the ground (Fig. 2B), rotted quickly, and disappeared within one year. Even the hard woody crowns of the decline plants rotted quickly. In contrast, at healthy sites, or at sites sprayed with herbicide, the dead stems often stayed hard and upright for two to three years.

Application of the fungicide did not protect the plants in the decline site from further decline to near zero values by 2008. Since the fungicide is specific to true fungi (ascomycetes and basidiomycetes), we considered the decline might be caused by one or more oomycetes, such as *Phytophthora.*

Surveys to Determine Extent and Distribution of the Decline Syndrome

All surveys were made between 15 March 2011 and 22 March 2012 by at least two observers and always included Lee Fontanini. A hand-held global positioning system (GPS) unit (GARMIN GPS, eTrex, high sensitivity) was used for geo-referencing and mapping. Date, location, waypoint number, and coordinates were recorded at the start and end of an assessment area and when plant condition changed. The following were also recorded separately for each river bank: health of blackberries (1 = healthy/vigorous, 1–2 = signs of poor vigor, 2 = plants stressed by foliar pathogens or grazing, 2–3 = evidence of recent herbicide use, 3 = dead or dying due to decline); density ([percentage of vegetation cover] 1 = absent, 2 = <1%, 3 = 1–10%, 4 = 11–50%, 5 = >50% on the riverbank); and any photo numbers and comments. The riparian zone across both sides was up to 100 m wide (but usually about 30 m wide) and is clearly defined both by a distinct change in ground height (up to 2 m) and in the vegetation changing from riparian species to either karri or other forest types along with an associated change in soil type. Both sides of the river were assessed at the same time (these rivers are often not very wide and reduced to about 1 m in summer). Walking surveys were carried out in the area where the major decline was observed at the few road crossings, covering a distance of about 40 km of river (80 km of river bank).

Spot surveys along the rest of the river were made at vehicle access points. A waypoint was taken at the vehicle crossing/access point, and surveys of both sides, 100 m upstream and 100 m downstream from the crossing/access point, were made on foot. The same information was recorded as described for the walking surveys.

Collected data and points from GPS were imported to ArcGIS, ArcMap v. 10.0 (ESRI, Redlands, CA, USA), and maps (Figs. 3 to 5) were created. Blackberries are found extensively along both the Donnelly and Warren rivers, and along tributaries such as the Lefroy Brook (Figs. 3 and 5). The distribution of blackberries is limited by the 750 to 800 isohyet, as shown by the distribution on the Tone, Perup, and Donnelly rivers (Fig. 3). Blackberry is found downstream, almost to the coast, and into areas where the rainfall has averaged 1,600 mm (p.a.). Throughout this area, the blackberry has a cover of over 50%, typically forming dense thickets up to several meters high.

The initial two locations where decline was detected are 29 km apart on the Donnelly and Warren rivers (Fig. 3). The decline areas (Fig. 4) were found throughout the distribution of blackberry in the

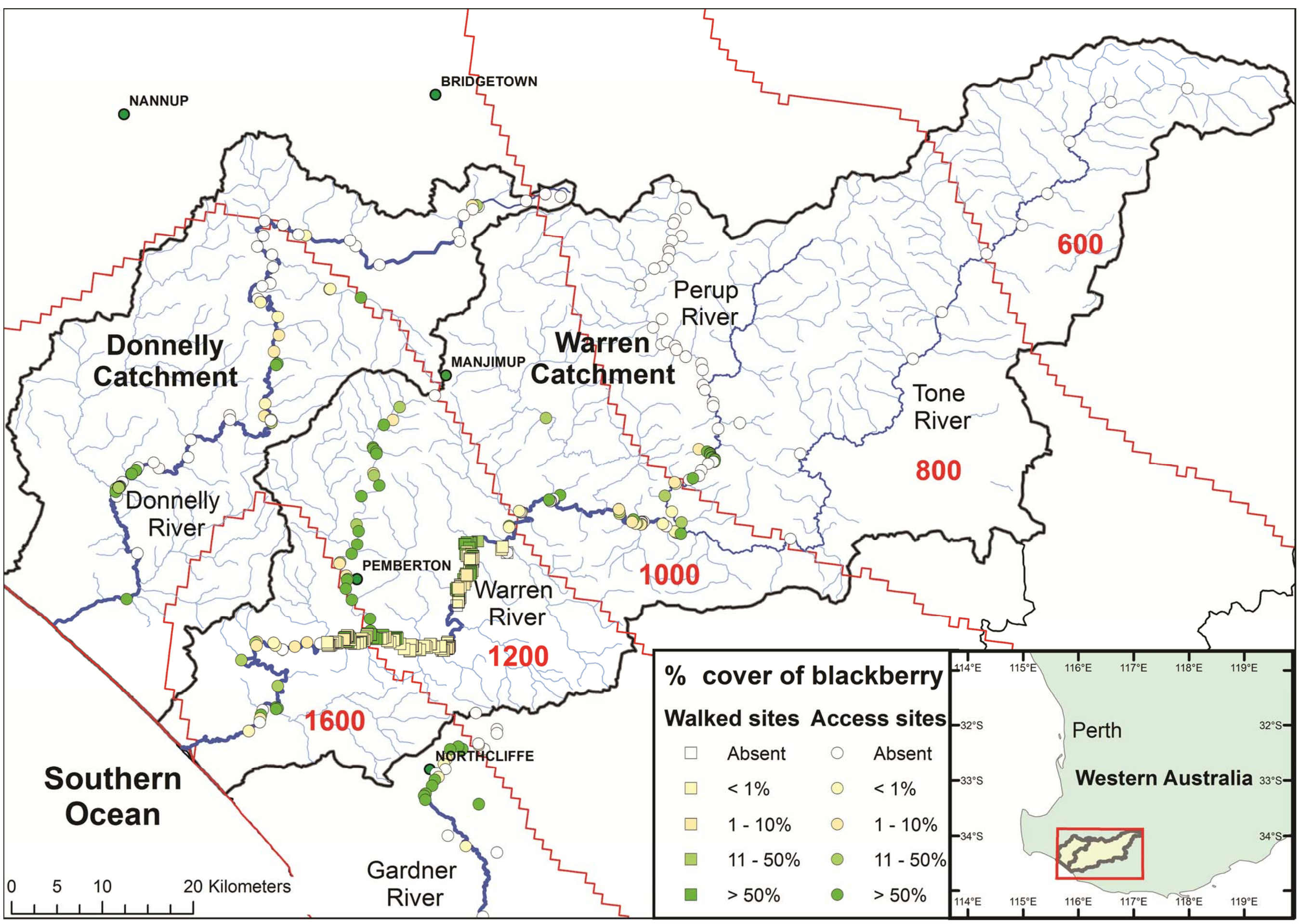

Fig. 3. Distribution of blackberry and its density along the Donnelly and Warren rivers and major tributaries during walked (Walked sites) and river crossing surveys (Access sites) in 2011 to 2013. The red zigzag lines and numbers show bands of average annual rainfall in millimeters. Walked sites (squares) are shown in more detail in Figure 5.

Donnelly and Warren Catchments, covering over 50 km of riverbank on the Warren River and 14 km on the Donnelly River (almost certainly an underestimate because large sections of the Donnelly River have not been surveyed). So far, the disease is mostly found along the major watercourses, probably in part due to the difficulty of accessing the densely forested areas.

For the walked sections of the Donnelly and Warren rivers with only native forest, decline presence was extensive, but not equivalent on both sides of the river. Distinct disease fronts were present, and these extended over time (Fig. 5).

A preliminary search in the neighboring catchment, the Shannon, returned only very healthy blackberries. The catchment to the north (the Blackwood) was subjected to widespread community releases of the rust fungus, and stakeholders were asked to respond with information on the effectiveness of the rust releases. No reports of decline from rust release or other causes were received. Further afield in Western Australia, dying blackberries have been reported, but have since proved to be due to the rust being particularly effective in certain seasons and locations.

Description of the "Blackberry Decline" Syndrome

At each decline and nondecline site, plants were visually assessed for disease symptoms and other stress factors before digging roots and soil samples. Decline symptoms included a dramatic change in the dense stands of blackberry and browning of the canes and foliage compared with healthy sites. Dead canes fall on the ground or remain 2 to 3 m high in forks of native trees. Dying and healthy plants were collected from adjacent declining and nondecline sites, respectively. Diseased and healthy roots and crowns were examined using a sharp scalpel to make horizontal and vertical slices to observe length and depth of lesions in the plant tissues, presence or absence of discoloration and necrosis, pathogen fruiting bodies, and insect activities. Since no evidence of disease was observed in canes, these were excluded. Crowns and roots were kept in the plastic bags in insulated boxes and moved to the laboratory for further processing. Crowns and roots were rinsed with tap water to remove soil particles, and root symptoms were assessed, photographed, and recorded. Crowns, roots, and soil materials from healthy and diseased plants were baited and plated on different selective and nonselective media in order to isolate possible pathogens (2). Several *Phytophthora*. (only from decline and adjacent sites), *Pythium,* and *Cylindrocarpon* species (from both decline and healthy sites) were recovered (1,2).

No lesions were observed in healthy blackberry roots and crowns (Fig. 6A and B), which were white internally compared with reddish-purple discoloration of coarse roots and crowns together with gray to black streaks in the vascular tissues of declining plants (Fig. 6C and E). The roots and crowns of dead plants affected by root rot showed dark chocolate brown to black necrotic lesions in all parts of the roots including fine roots, root hairs, and root tips (Fig. 6D and F). Necrosis of lateral roots was seen where they are attached to the main roots. The cortex of diseased roots could be sloughed off with ease in all diseased plants (Fig. 6F). Root biomass and production of root hairs was greatly reduced, and in most of the symptomatic roots, shortened root clusters were formed.

Canes that had been defoliated through rust infection, thrips damage, and activity of secondary fungi were observed. The impact of the decline on seeds in the soil was not measured. Likewise, it is not known if the decline affects seed in the soil. No

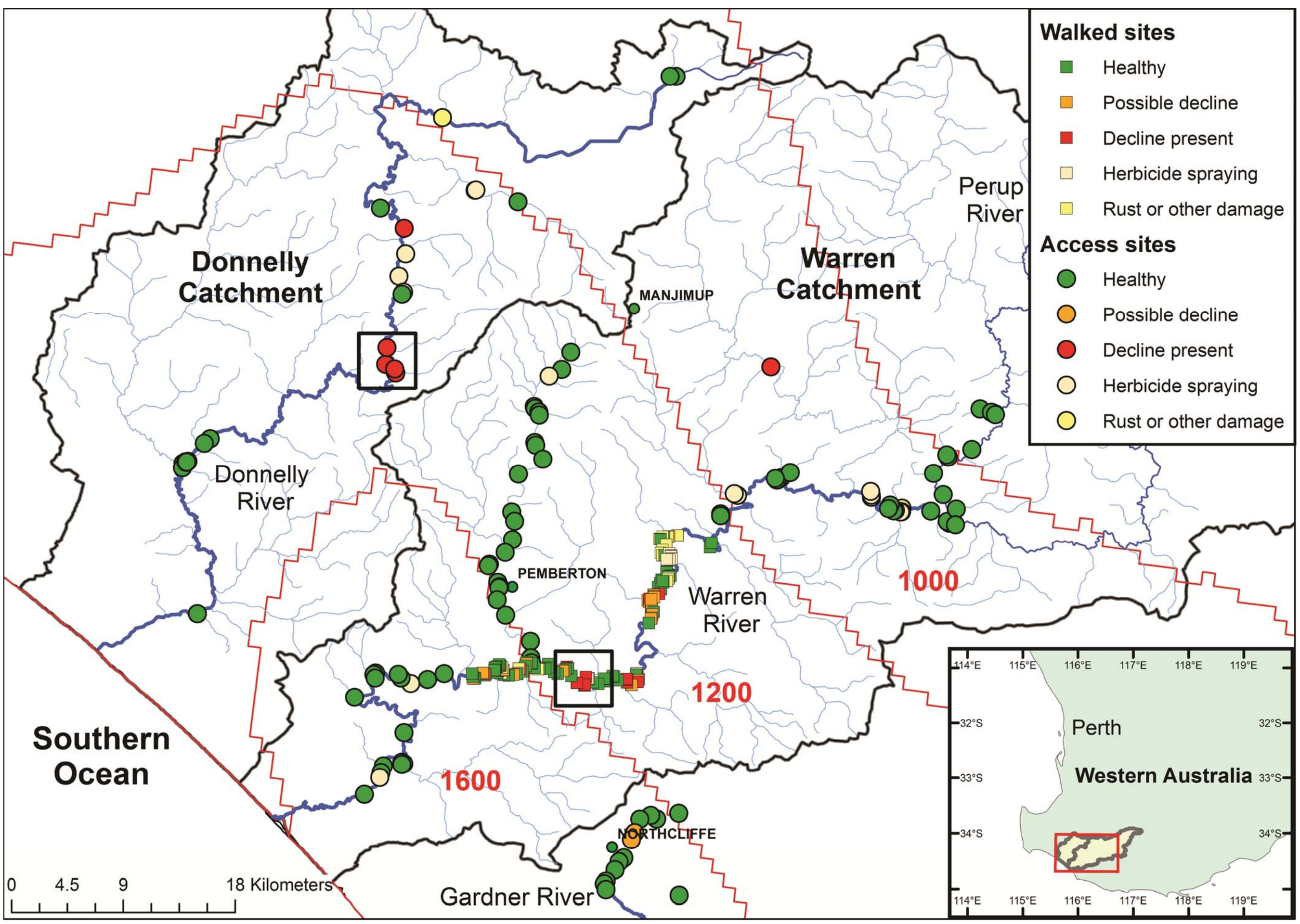

Fig. 4. Distribution of decline symptoms (red dots and squares) and other types of damage to blackberries observed along the Donnelly and Warren rivers and tributaries during walked and river crossing surveys in 2011 to 2013. The black squares show the location of the first two discoveries of blackberry decline. The red zigzag lines and numbers represent bands of average annual rainfall in millimeters. Walked sites (squares) are shown in more detail in Figure 5.

mortality of seedlings was observed in decline areas; however, at most of the sites there was very little if any seedling development observed.

Comparison with Herbicide-Affected Plants

Populations of blackberries dying due to herbicide can initially look very similar to those dying due to the decline syndrome. In both cases, the crowns of dying plants can look similar, with the red-purple layer being present. However, herbicide-treated canes are hard and woody and persist for up to three years, while those killed by the decline syndrome are soft and disappear from the site within one year. In addition, herbicides are not specific to blackberry, so off-target damage occurs and is usually evident on adjacent native plant species. This "collateral damage" was not observed in decline sites.

Blackberry Decline Conceptual Model

We have identified numerous factors that may contribute to the decline. These are summarized in the blackberry decline conceptual model (Fig. 7) showing a decline spiral (34,39). Other components included in our spiral were based on our observations and from the literature. The factors are grouped into predisposing, inciting, and contributing factors.

Predisposing factors. Climate or site factors are always a major predisposing component to a decline syndrome (39). In SWWA, the climate is expected to become warmer and dryer, but with more extreme weather events (43). Wildfires in natural ecosystems in Australia kill blackberries and allow natives and other competitor species to grow (50). Furthermore, the topography of the *R. anglocandicans* decline sites consists of broad river valleys facilitating cyclic inundation following large rainfall events (including rainy days over summer), which raise the water levels in the Donnelly and Warren rivers, often causing temporary flooding. These flooding events can last for 10 days or more and will lead to temporary waterlogging of the riparian zone (flood plain) normally above the water level. In contrast, in the nondecline sites where temporary inundation does not occur, *R. anglocandicans* remains healthy. Occasional dense stands of *R. anglocandicans* were observed on steep, well-drained banks of rivers in the decline sites, which further supports the "waterlogged soil" predisposition hypothesis underlying the decline syndrome. Blackberries do not like waterlogging (17), and this stress predisposes them to infection by root pathogens. Flooding also distributes soilborne pathogens and their propagules.

Shading and low light reduce photosynthesis, which in turn stresses plants and eventually causes mortality due to carbohydrate starvation (41,45,62). A combination of shading with mechanical abrasions and other factors can alter photosynthate allocation (62) and susceptibility to root pathogens. For instance, Matson and Waring (42) have demonstrated a significant relationship between shading and susceptibility of mountain hemlock (*Tsuga mertensiana*) forests in the Oregon Cascades to dieback and laminated root rot caused by *Phellinus weirii*.

Predisposing stress components are long-term factors in the conceptual tree decline model (34,39), and have the potential to enhance susceptibility of healthy plants to pathogens or injury-inducing factors. These stresses set the stage for inciting factors (11).

Inciting factors. Lack of genetic potential has been recognized to have a role in blackberry decline. In a few taxa within the Rosaceae such as *Rubus alceifolius* (5) and *R. anglocandicans* (25), the reproduction system is mainly apomictic. As an introduced species, the founder population of *R. anglocandicans* in Australia already had low genetic variability, which is confounded by the apomictic reproductive system (25). Vegetatively propagated species with self-pollination are generally more severely attacked by diseases than cross-pollinating ones (16,32); therefore, in Australia a lack of genetic potential in *R. anglocandicans* populations is likely to have a strong involvement in the decline syndrome.

Grazing may also be an inciting factor, and ringtail possums (*Pseudocheirus occidentalis*), quokkas (*Setonix brachyurus*), and grey western kangaroos (*Macropus fuliginosus*) were photographed grazing in blackberry sites (L. Fontanini, *personal observations*).

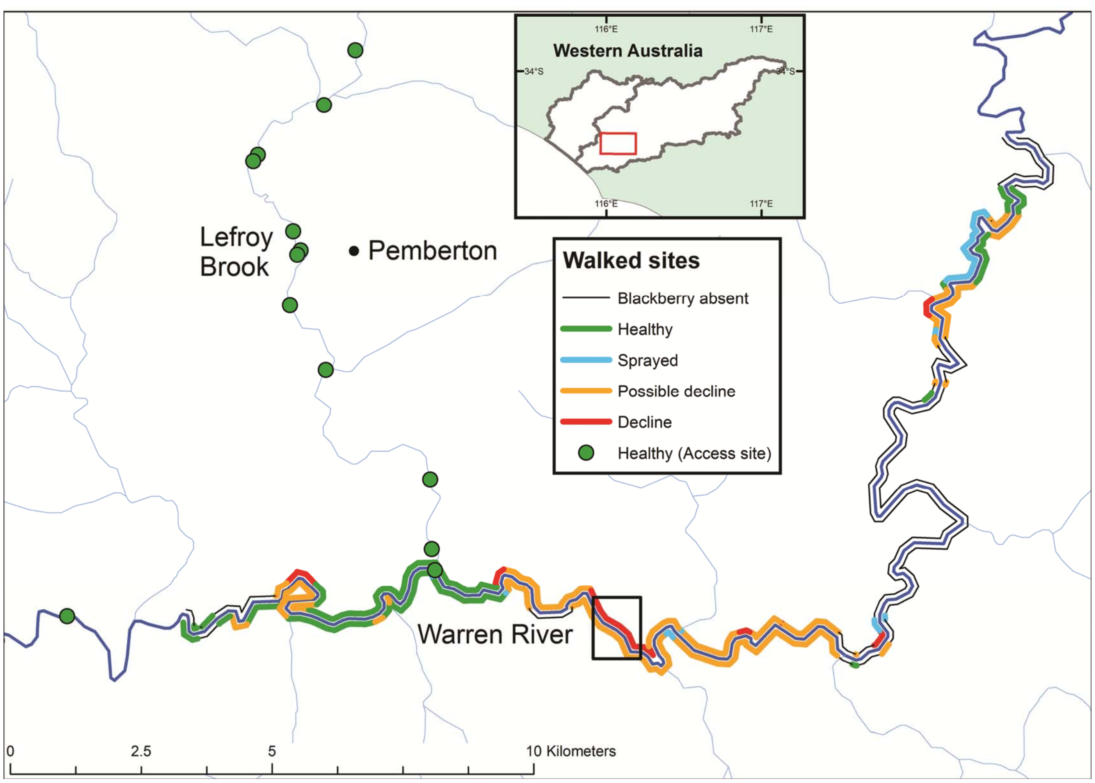

Fig. 5. Distribution of blackberry decline symptoms along a section of the Warren River detected during walked surveys in 2010 to 2011. Nearby Access sites surveys (Fig. 4) are shown as dots. Plant absent: 30.72 km; plant healthy: 15.50 km; plant sprayed: 2.98 km; possible decline: 26.03 km; plant decline: 4.18 km; total Riverbank: 79.41 km (i.e., 39.71 km of Warren River surveyed by walking).

Exotic mammals (goats) were also captured on camera feeding on blackberry. The role of herbivores and overgrazing in similar scenarios was illustrated in a recent study by Elmer et al. (18) on sudden vegetation dieback in Atlantic and Gulf Coast salt marshes.

Competition of native species and other invasive weeds for water, nutrients, and light should not be ignored. Competition with other introduced species was listed as a cause for population crashes of four invasive species showed by Simberloff and Gibbons

Fig. 6. Healthy blackberry crowns and roots **(A and B)** and blackberry decline symptoms **(C to F): A,** longitudinal section of a healthy crown with cream to white tissues; **B,** healthy root ball; **C,** reddish-purple discoloration in a crown; **D,** a diseased root with dark chocolate brown to black necrotic lesions in all parts of the roots; **E,** gray to black streaks in the vascular tissues; **F,** severe root damage with cortex sloughing off symptoms (arrows).

(57). Native bracken (*Pteridium esculentum*) and sedges (*Lepidosperma effusum*) can be considered as competitors in blackberry infested sites in the SWWA (L. Fontanini, *personal observations*).

Slashing or mowing (removal of live top-growth) is one of the Integrated Weed Management (IWD) strategies to control the blackberry population in Australia (10,50). It forces the plant to regrow and may deplete crown and root reserves. Consequently, plants become more susceptible to death from other causes. Furthermore, during summer, the impact of blackberry leaf rust can be enhanced as juvenile leaves and newly emerged foliage (present as the consequence of slashing) are more susceptible to the rust isolates (10,50). Controlled burns before herbicide application are also used to reduce blackberry thickets to a more manageable size, and burning after herbicide spray clears away dead canes (50).

The application of herbicides can induce root disease problems (38) and other diseases of plants (36). For example, fungal colonization of tomato roots occurs rapidly after glyphosate is applied (7). Furthermore, a combination of a low dose of glyphosate together with *Cylindrocarpon destructans*, a natural colonizer of roots of thimbleberry (*R. parviflorus*), caused mortality and wilting of the plants (61).

Contributing factors. Leaf rust (*P. violaceum*) has been identified as a successful biological control tool in some locations in Australia with direct and indirect impacts on blackberry growth. Continuous attack on the leaves by such fungal foliar pathogens weakens plants by depleting root reserves of photosynthates. Leaf rust infection during sequential growing seasons can lead to more defoliation and allow other plants to compete particularly over autumn and winter, when blackberries are in a dormant stage, which in turn can limit blackberry growth through shading (9). Stem rust caused by *Kuehneola uredinis* (56) has less impact on blackberries. Thrips damage (common greenhouse thrips: *Heliothrips haemorrhoidalis*) was regularly observed and can lead to blackberry defoliation. Red berry mite (*Acalitus essigi*) (55) and leaf spot (*Septoria rubi*) (17) were recorded regularly and can weaken blackberries or reduce seed dispersal.

In the decline sites, gray mold caused by a *Botrytis* sp. and other secondary fungi grew on leaves and canes of *R. anglocandicans* containing stem and leaf rusts. Synergistic effects have been observed between necrotrophic fungi and rusts resulting in more rapid cell death (15,29). Secondary pathogens invade rust (*Puccinia poarum*) pycnia and aecia on coltsfoot (*Tussilago farfara*), which has led to death of host leaves (15).

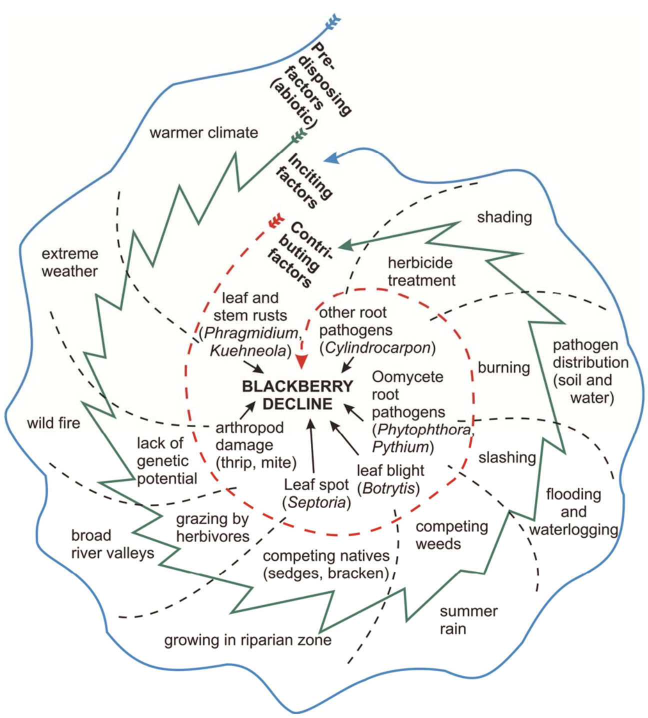

Fig. 7. Conceptual model of possible factors involved in blackberry decline (based on the tree decline model of Manion [39]).

During our disease surveys, eight *Phytophthora* species were isolated from decline sites, including *P. amnicola*, *P. bilorbang*, *P. cryptogea*, *P. inundata*, *P. litoralis*, *P. multivora*, *P*. taxon *personii*, and *P. thermophila*. *P. bilorbang* together with *P. cryptogea* was recovered consistently from baited roots and associated rhizosphere soil collected from decline and adjacent declining sites over different seasons. Furthermore, different *Pythium* species, *Cylindrocarpon destructans*, and *C. pauciseptatum* were also recovered more commonly from blackberry decline sites than from nondecline sites. The involvement of different *Phytophthora* species has been assessed through laboratory, glasshouse, and field trials, and the strong association of *P. bilorbang* (2) and *P. cryptogea* in the blackberry decline has been postulated (*unpublished data*). However, the possible synergism between different *Phytophthora* species and other weak pathogens should not be ignored. Synergism between *Phytophthora* spp. and *C. destructans* has been demonstrated for black foot in grapevine (28). Moreover, in other disease complex scenarios such as apple replant disease, Tewoldemedhin et al. (58) have highlighted the importance of synergistic interactions between recovered *Phytophthora, Pythium,* and *Cylindrocarpon* species using co-inoculation approaches. Hence, we are investigating interactions between putatively pathogenic *Phytophthora* species and *C. pauciseptatum* in an ongoing soil-infestation pot trial in the glasshouse.

Phytophthora species are best known as invasive pathogens destroying trees and crops worldwide. Plant diseases caused by *Phytophthora* species are devastating to agriculture and natural ecosystems (31,37). As of 2012, there are 121 described *Phytophthora* species with 4,384 distinct host–pathogen associations distributed in 138 countries (53). *Phytophthora* species are one of Australia's most serious plant pathogens, and the majority of *Phytophthora* species have been introduced to Australia and widely distributed (35). We believe that oomycetes, and in particular *P. bilorbang* and *P. cryptogea,* have strong involvement in the blackberry decline and are able to cause severe damage to the roots after temporary inundation creating conducive conditions in the declining sites across the Donnelly and Warren rivers. The host range of *P. bilorbang* is unknown, as this species has only been recently described (2); whereas *P. cryptogea* has a worldwide distribution and wide host range (19) and has been reported on raspberry in Australia (63). Even so, the only two cases of mortality on hosts other than blackberry were observed in *Eucalyptus patens* and *Banksia littoralis,* and these were associated with *Phytophthora cinnamomi*. Water-logging in conjunction with invasion by *Phytophthora* species may be especially effective, and thereafter *Cylindrocarpon* species may invade the weakened roots and produce toxins as has been postulated by Unestam et al. (59).

Plants mediate interactions between different above- and belowground biota and respond to stressors in several ways. Eventually these responses may result in negative effects on the plant itself (33). We believe that contributing factors included in the blackberry decline spiral all have a role in this syndrome, but the involvement of the hypothesized predisposing and inciting factors is also essential for the expansion of the decline.

Summary

Blackberry decline is now a major feature in the ecology and control of blackberry, with an impressive impact on previously infested banks along the Donnelly and Warren rivers. To date, there are no reports of blackberry decline in neighboring catchments (e.g., Shannon, Blackwood). Likewise, we are not aware of any similar "decline" syndromes from elsewhere in the world, despite blackberry being a very widespread species. Therefore, to our knowledge, this is the first record of such a decline of European blackberry (*Rubus anglocandicans*) worldwide. At this stage, we have not observed any deaths of native plants in areas where blackberry decline is present. Worldwide decline syndromes are being observed in natural ecosystems (18,43,44), and the conceptual approach that we have adopted could have wider applicability. More work is required to understand the decline syndrome to determine if severely infested riparian zones can be manipulated to initiate the decline syndrome as a management tool for blackberry control. This would require detailed assessment of the host range of the pathogens involved, including susceptibility of plant species to be used in restoration of decline sites. The biotic (contributing) factors discovered in this research have yet to be investigated in more complex trials to examine their interactions in conjunction with other stress enhancing factors. Another challenge is to manage these decline sites, to ensure the return of native riparian species and to prevent other exotic weedy species replacing blackberry. Finally, if other invasive plant species are observed to be in decline, we believe the approach we have taken together with the "decline spiral" offer useful tools to help others determine the causes.

Acknowledgments

We thank the Western Australian Department of Parks and Wildlife, Western Australian Department of Agriculture and Food, the Manjimup Shire Council, the Warren Catchments Council, CSIRO, Murdoch University, and Rural Industries Research Development Corporation for support and funding. We appreciate Dr. Laurence A. Mound for identifying the thrips and Emeritus Prof. Jen McComb for her valuable comments on the manuscript.

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Ms. Fontanini is a project manager at the Warren Catchments Council and has been involved in native flora assessments and weed management across Western Australia. She is the Community Member on the Australian Blackberry Taskforce and has been involved with blackberry for more than a decade, managing control programs and conducting extensive field surveys, and is responsible for the native revegetation project in areas of blackberry decline along the Warren and Donnelly rivers.

Mr. Yeoh is a research officer at CSIRO. He is involved in research on weed ecology and management in Western Australia with an emphasis on conducting laboratory and field experiments. He has been involved with blackberry for the past decade, releasing biological agents targeting this weed and monitoring the plant's growth and impact with or without various control measures.

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