Key lessons from resistant tree breeding programmes in the Northern Hemisphere

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Abstract

• *Key message* To inform emerging initiatives, we explored five programmes that aimed to develop trees resistant to specific pests or pathogens. These case studies show resistant tree programmes are a medium to long-term approach requiring sustained investment, and can encounter substantial difficulties in developing and maintaining resistance. Equally, adequately resourced and well-planned programmes have resulted in operational deployment of resistant trees.

• *Context* Developing trees that are resistant to specific pests and pathogens is an increasingly prominent strategy for responding to this escalating threat. It is therefore important to ensure decisions to use resistant trees and approaches to development are well-informed.

• *Aims* We aimed to provide insights for newer or proposed resistant tree breeding programmes by identifying key lessons from earlier programmes, some of which date back several decades.

• *Methods* We selected five mature programmes as case studies, and in each case synthesised information from key publications and by following citations to original sources. We examined the objectives, methods, problems, successes and timescales in each programme.

• *Results* Resistant tree breeding is generally a medium to long-term approach requiring sustained investment and co-ordination, although culturally valued species can attract considerable support from volunteers. Deployment of resistant trees often recommends maintaining genetic variation and mixing with other tree species. Substantial costs and loss of confidence in future material can arise if resistance breaks down or resistant material is susceptible to other threats.

• *Conclusion* The case studies illustrate success is not guaranteed, but also provide evidence that adequately resourced and well-planned resistant tree programmes can contribute to strategies to mitigate impacts from pests and pathogens.

Keywords Tree breeding · Fungi · Herbivore · Insect · Disease · Forest management

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1 Introduction

Pathogens and arthropod herbivores are integral parts of natural forest ecosystems but can also cause widespread damage and mortality in managed and unmanaged forests. These impacts can be very severe, particularly where trees have few evolved defences because the pathogen or herbivore is not present within the native range of the tree (Boyd et al. 2013; Brasier 2008). For example, the Asian fungal pathogen chestnut blight (*Cryphonectria parasitica* [Murr.] Barr) killed billions of chestnut trees (*Castanea dentata* [Marsh.] Borkh.) following accidental introduction to North America, causing fundamental shifts in the composition and functioning of forest ecosystems and removing a potentially valuable timber

resource (Jacobs 2007; Jacobs et al. 2013). Native pests and pathogens can also have important sustained or periodic impacts with high levels of mortality and damage (Aukema et al. 2006). The risks from non-natives are increasing as globalised trade networks facilitate spread, and the impacts from both native and non-native organisms may be amplified by other anthropogenic influences (Pautasso et al. 2012). Reflecting the scale of past and potential future impacts, combating pests and pathogens is thus an increasingly important concern (Freer-Smith and Webber 2015).

Although preventing and controlling pest and pathogen spread is important, this is often only a partial solution. As such, developing trees that are resistant to specific organisms is receiving new impetus—e.g. preliminary evidence that some ash trees may be less susceptible to ash dieback (*Hymenoscyphus fraxineus* [T. Kowalski] Baral, Queloz, Hosoya) is stimulating interest in several countries in using these trees to breed a resistant population (Defra 2013; Vasaitis and Enderle 2017). It is therefore important to understand where and how resistant tree programmes can be most effectively implemented and what the expectations should be. Note that for brevity, we refer to 'resistant tree programmes'—this potentially encompasses several related concepts (Sniezko and Koch 2017), including complete resistance (trees are fully resistant to a given organism and suffer minimal impacts), partial resistance (trees have mechanisms to reduce attack but suffer some impacts) and tolerance (trees get attacked/infested and display symptoms, but are nonetheless able to maintain growth and performance more effectively than less tolerant individuals).

Insights from recent review articles can help to inform decisions on whether resistant tree programmes should be pursued elsewhere, and on what the approaches, requirements and expectations should be. For example, Sniezko and Koch (2017) highlight the opportunities and challenges presented by the emergence of new technology such as improved DNA sequencing methods and (potentially) genetic engineering, whilst Woodcock et al. (2018) describe a general framework for the processes and decisions involved in developing and using resistant trees, from initial screening through to operational deployment. Whilst recognising the potential importance of resistant trees, both studies also note the need to learn from previous experiences. However, the key events in resistant tree programmes are often dispersed across many publications. Furthermore, there is relatively little direct comparison amongst programmes of the different approaches used, or evaluation of why some efforts appear to have been more successful or rapid than others. Such comparisons could help guide the strategies of emerging and proposed resistant tree programmes, particularly if accompanied by timelines indicating key events. As such, here we

investigate several case studies from temperate and boreal systems, and ask the following questions:

(i)   What different approaches are used for screening, developing, producing and deploying resistant trees, and how are these influenced by biological factors (e.g. frequency of resistance within tree population) and stakeholder motivations (e.g. ecological vs. economic)?
(ii)   What are the timescales over which key events in resistant tree programmes occur?
(iii)   What problems have been experienced by resistant tree programmes, and what strategies have been used to mitigate these problems?
(iv)   What factors influence the success of resistant tree programmes?

2 Methods

2.1 Selecting case studies

We aimed to identify resistant tree programme case studies from temperate or boreal systems that collectively encompassed the following criteria:

- Tree breeding against pests and against pathogens
- Tree breeding against native and against non-native threats
- Conifer and broadleaf species
- Differing motivations for tree breeding programme (e.g. economic, ecological, cultural etc.)

We focused on case studies that have been in place for several years, rather than less established programmes from which the ability to understand timescales, successes and problems is more limited. We also required programmes in which it was possible to clearly describe key stages and processes (see *Data Extraction*). To find case studies, we initially consulted a review carried out by the Food and Agriculture Organisation (FAO 2013) documenting the status of 274 resistant tree programmes (http://www.fao.org/forestry/26460/en/). However, in the 2013 update of this review, many resistant tree programmes were incomplete (only 44 had established breeding programmes, of which 23 were planting material operationally). Furthermore, preliminary investigation of the literature linked by the FAO database illustrated wide variation amongst programmes in the amount of information provided and in the ease with which this could be accessed. As such, some resistant tree

programmes are more tractable for detailed exploration than others, and more likely to generate useful insights.

To select case studies, we used a combination of the resources linked by the FAO database and our own knowledge to identify programmes that collectively encompassed the criteria outlined above and for which our initial investigations indicated that sufficient information could be obtained. Links and resources associated with this exploration are provided in Table 1 for information. The non-systematic nature of our case study selection means that our findings are illustrative of some of the different contexts, approaches, timescales and types of problems, rather than representative of *all* attempts to develop resistant trees. The case studies used were as follows: (1) American chestnut and chestnut blight—The American Chestnut Foundation, (2) American chestnut and chestnut blight—American Chestnut Co-operators Foundation, (3) Sitka spruce (*Picea sitchensis* [Bong.] Carr) and white pine weevil (*Pissodes strobi* Peck (Coleoptera: Curculionidae)—British Columbia Ministry of Forests, (4) Western white pine (*Pinus monticola* Douglas ex D. Don) and white pine blister rust (*Cronartium ribicola* J.C. Fisch)—several programmes, and (5) several elm species (*Ulmus* spp.) and Dutch elm disease (*Ophiostoma novo-ulmi* [Brasier])—Italian Institute of Plant Protection. Although we did not specifically exclude the Southern Hemisphere, the European and North American locations of our case studies mean that the findings are likely to be most informative in these systems.

2.2 Data extraction

To facilitate comparison between case studies, we extracted and collated data based on six steps previously identified as necessary components of resistant tree programmes (Woodcock et al. 2018; Table 2). The first step (1) describes the scope, context and objectives of the programme. Subsequent steps then detail the approach to (2) finding resistant trees, (3) breeding for resistance, (4) large-scale production, and (if relevant) (5) planting resistant trees in the field, and (6) subsequent monitoring of performance. We also gathered information on the timing of important events in the

Table 1 Tree-pest/pathogen systems from which case studies were selected. Not intended to be comprehensive (see http://www.fao.org/forestry/26460/en/ for further examples). Also note that several programmes may not yet have reached deployment stage

Tree species	Pest or pathogen	Programmes
American chestnut (*Castanea dentata*)	Chestnut blight (*Cryphonectria parasitica*)	The American Chestnut Foundation[1] The American Chestnut Co-operators Foundation[2] Connecticut Agricultural Experimentation Station[3] American Chestnut Research and Restoration Project[4]
Sitka spruce (*Picea sitchensis*)	White pine weevil (*Pissodes strobi*)	British Columbia (B.C.) Ministry of Forests, Pacific Forestry Centre and B.C. universities[5,6]
Several susceptible *Ulmus* spp.	Dutch elm disease (*Ophiostoma ulmi*; *Ophiostoma novo-ulmi*)	Willie Commelin Scholten Phytopathological Laboratorium[7] Italian Institute of Plant Protection[7,8] US Forest Service[7,9] University of Minnesota[7,10] Morton Arboretum[7,11] The Great British Elm Search[12]
Several susceptible *Pinus* spp.	Blister rust (*Cronartium ribicola*)	US Forest Service[13–15] B.C. Ministry of Forests[16]
American beech (*Fagus grandifolia*)	Beech bark disease (*Nectria coccinea*)	USDA[17,18]
Butternut (*Juglans cinerea*)	Butternut canker disease (*Sirococcus clavigignenti-juglandacearum*)	USDA[19–22]
Several susceptible *Pinus* spp.	Dothistroma needle blight (*Dothistroma* spp.)	CEH, Forestry Commission, Forest Research[23] CSIRO[24]
Several susceptible *Fraxinus* spp.	Emerald ash borer (*Agrilus planipennis*)	USDA[25]
N. American hemlock species (*Tsuga* spp.)	Hemlock woolly adelgid (*Adelges tsugae*)	USDA[26–28]

Further information available at:

[1] The American Chestnut Foundation (http://www.acf.org). [2] The American Chestnut Co-operators Foundation (http://www.accf-online.org). [3] Connecticut Agricultural Experimentation Station (www.ct.gov/caes). [4] College of Environmental Science and Forestry (http://www.esf.edu/chestnut). [5] King et al. (2004). [6] Alfaro et al. (2013). [7] Mittempergher and Santini (2004). [8] Santini et al. (2012). [9] Townsend et al. (2005). [10] University of Minnesota (https://www.legacy.mn.gov/projects/finding-disease-resistant-elm-trees-minnesota). [11] Morton Arboretum (http://www.mortonarb.org/trees-plants/tree-plant-descriptions/elm-cultivars). [12] The Conservation Foundation (https://www.conservationfoundation.co.uk/elms). [13] Fins et al. (2001). [14] McDonald et al. (2004). [15] Sniezko et al. (2008). [16] British Columbia Ministry of Forests (http://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/tree-seed/forest-genetics/tree-breeding-improvement/western-white-pine). [17] Koch (2010). [18] Koch et al. (2012a). [19] Michler et al. (2005). [20] Woeste et al. (2009). [21] McKenna et al. (2011). [22] Boraks and Broders (2014). [23] Perry et al. (2016). [24] Ivkovic et al. (2011). [25] Koch et al. (2012b). [26] Bentz et al. (2008). [27] Montgomery et al. (2009). [28] Oten et al. (2014)

Table 2 Intended information on resistant tree programmes to extract from case studies

Scope and objectives	Organisation(s)	
	Region	
	Tree species	
	Pest or pathogen	
	Severity	
	Main impacts	
	Programme objectives	
Timescales and costs	Estimated investment	
	Programme start date	
	Status	
Approach to screening	E.g. use of field surveys, planting trials etc.	
Approach to tree breeding	E.g. conventional tree breeding, hybridisation etc.	
Approach to producing material	E.g. seed orchards, grafting etc.	
Approach to deployment	Scale	
	Strategy	
Approach to monitoring	E.g. long-term screening trials, field tests, volunteer-led	
Problems	Noted problems and considerations	
Complementary approaches	Other approaches promoted by organisation to improve success of resistant tree programme	

programme, problems encountered and, where possible, costs. We obtained this information through key publications describing the status and/or plans for a given programme, supplemented by following any citations to original sources—the latter included journal articles, technical reports, newsletters and websites. The context for each case study is described in Box 1 and summarised in Table 3, with more detailed information in Tables 4 and 5.

Box 1 Context for selected resistant tree programmes

American Chestnut (*Castanea dentata*)–chestnut blight (*Cryphonectria parasitica*)

American Chestnut was a major part of eastern N. American forests with important effects on a range of ecosystem functions, as well as being a valuable timber source. However, the species was devastated by the accidental introduction of chestnut blight, a necrotrophic pathogen native to Asia that infects primarily through stem wounds. *C. parasitica* was first discovered in the USA in 1904 and spread rapidly causing very high mortality throughout the American Chestnut range. This had cascading impacts on forest structure, biodiversity and ecosystem functioning.

Comparing *C. parasitica* populations between North America and Europe (where it was also accidentally introduced) suggests there is greater genetic variation in the former. This is believed to reduce the effectiveness of hypovirulence as an alternative method of controlling the disease in N. America, and could have implications for resistance breeding. We focus on attempts to breed blight-resistant American Chestnut carried out by The American Chestnut Foundation (TACF) and by the American Chestnut Co-operators Foundation (ACCF).

European Elm species (*Ulmus* spp.)–Dutch Elm Disease (*Ophiostoma ulmi, O. novo-ulmi*)

Elms are generally fast-growing and particularly valued aesthetically. As such, the genus was used extensively in landscaping, including in urban areas with high levels of air pollution. However, two waves of Dutch Elm Disease (DED) had serious impacts on European and North American species. Thought to be native to Asia, the DED fungus is a vascular pathogen affecting several elm species and spread by the elm bark beetle. *O. ulmi* was first discovered in European elm species in the early twentieth century, and later accidentally introduced to N. America.

Sitka spruce (*Picea sitchensis*)–pine weevil (*Pissodes strobi*)

Sitka spruce is an important part of temperate North American forests. Its fast growth rate and good wood properties make it a commercially valuable timber species outside the native range. However, the use of Sitka spruce in North American forestry has been heavily constrained by the white pine weevil.

P. strobi is native to North America and does not generally kill trees. However, the resulting deformities reduce economic returns, and severe outbreaks can cause plantation failure due to poor wood quality. Genetic variation in *P. strobi* is high relative to other insects, and long-distance dispersal of the species appears to be rare. As such, there are several genetically distinct populations across the native range, some of which also contain substantial genetic diversity (Laffin et al. 2004). We focus on attempts to breed weevil-resistant Sitka spruce by the British Columbia Ministry of Forests.

Western White Pine (*Pinus monticola*)–white pine blister rust (*Cronartium ribicola*)

Western White Pine (WWP) was formerly widespread and ecologically important across mid-elevation forests in western North America. The species is well-adapted to seasonal climatic variation and is relatively fast-growing under suitable conditions, making it a potentially important timber species.

WWP is highly susceptible to White Pine Blister Rust (WPBR), a stem rust accidentally introduced from Europe in the early 1900s. Mortality to WPBR was very high, with WWP reduced to a fraction of its original

(continued)

Although. *O. ulmi* had substantial impacts in N. America, it did not devastate populations in Europe. However, a more virulent strain (*O. novo-ulmi*) to which there was very little resistance emerged on both continents during the 1960s, killing millions of trees. *O. novo-ulmi* displaces the less virulent *O. ulmi*, and has also acquired beneficial genes from the latter through interspecific hybridisation (Bernier 2017). Distinct *O. novo-ulmi* subspecies are now documented, along with subspecies hybrids that are also spreading across Europe. This case study considers the DED-resistance breeding programme by the Italian Institute for Plant Protection (IPP): note there are several other programmes in Europe and North America (Table 1)

cover by the 1960s. The WPBR pathogen has windborne spores that are particularly favoured by cool, moist conditions during summer and autumn. The life cycle of the organism also requires *Ribes* spp. Although introduced, WPBR is not genetically uniform, with outcrossing and (in more isolated populations) genetic drift contributing to genetic diversity. Genetic differences in WPBR affect virulence, and a variant strain of the pathogen is able to circumvent some mechanisms of resistance used in initial WWP tree breeding programmes. We decided to consider three North American programmes to breed for WPBR resistance, due to the overlap and linkages between these programmes.

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3 Results

3.1 Scope, objectives and co-ordination

Some resistant tree programmes are co-ordinated and funded primarily by government influence forestry departments, whereas others have substantial NGO involvement (often with government support) or commercial interest. These groups are motivated by many factors, from the national cultural significance of the species (e.g. American chestnut; Jacobs et al. 2013) through to the commercial value from timber production (e.g. Sitka spruce; Alfaro et al. 2013) or potential benefits from patenting resistant material (e.g. European elms; Santini et al. 2012). In the case of American chestnut, public engagement and interest is an important standalone objective. Context also varies, with some programmes aiming to restore a species that has already suffered a major decline (e.g. American chestnut-chestnut blight programmes; Jacobs et al. 2013), whilst others focus on minimising ongoing impacts (e.g. Sitka spruce-pine weevil; Alfaro et al. 2013). These differences in motivation and context influence the resources available and the approaches taken in subsequent steps.

3.2 Finding resistant trees

Initial evidence of resistance in the case studies came from relatively ad hoc field observations. These early findings shaped subsequent work, either by identifying potentially resistant material for further trials (Alfaro et al. 2013) or informing an emphasis on resistant hybrids rather than relying on very rare within-species resistance (Santini et al. 2012; Jacobs et al. 2013). All the case studies used planting trials to further investigate potential resistance, often including susceptible families as controls (Sniezko et al. 2014). In some trials, the pest or pathogen is deliberately introduced to expedite the test and standardise comparison across sites, and heritability and geographic differences in resistance are explored (Alfaro et al. 2013). Trials also often revealed important complexity in the expression of resistance—e.g. multiple resistance mechanisms influenced by environmental factors and tree age (Hebard 2005a; King et al. 2010). Lastly, the time,

costs and land involved in planting trials are often substantial, meaning considerable resources and co-ordination can be necessary (Alfaro et al. 2013).

3.3 Approaches to developing resistance

Two general approaches were used to breed resistant trees. Where observations suggested some resistance, conventional breeding between individuals of the same species was preferred (e.g. rust resistance in Western White Pine [WWP] and weevil resistance in Sitka spruce; Alfaro et al. 2013; Sniezko et al. 2014). By contrast, the American chestnut and the elm breeding programmes use hybridisation between susceptible species and a resistant relative, reflecting evidence that very few individuals of the affected species appear resistant to these diseases. Tree breeding approaches are also shaped by the rationale for the programme, to the extent that more complex or time-consuming methods are sometimes preferred. For example, The American Chestnut Co-operators Foundation (ACCF) aims to develop blight-resistant pure American chestnut (www.accf-online.org) despite the rarity of resistance within the species. The approach involves controlled crosses of surviving trees (as well as open pollination of survivors) coupled with the use of hypovirulent strains of *C. parasitica* for blight control (Griffin et al. 2005). Similarly, although The American Chestnut Foundation (TACF) produced a blight-resistant hybrid many years ago (Fig. 1; Diskin et al. 2006; Jacobs et al. 2013), the organisation is committed to restoring the ecological and cultural importance of American chestnut and so uses several generations of backcrossing (combining the hybrid with American chestnut parents) to recover characteristics of the pure species (Jacobs et al. 2013). Subject to regulatory approval, TACF also intend to incorporate genetically engineered trees into the breeding programme (Westbrook 2018). This material contains the oxalate oxidase gene, which confers resistance to *C. parasitica* by detoxifying oxalate produced by the pathogen (Steiner et al. 2017). Again however, rather than plant genetically engineered trees immediately, TACF plan to use further breeding to dilute the contribution from the modified clone, as well as to incorporate resistance

Table 3 General characteristics of each case study. Black cells indicate a characteristic is highlighted by a given programme, grey cells: partly relevant, white cells: not highlighted in the literature consulted

			Programme				
			TACF[1]	ACCF[2]	B.C.[3]	IPP[4]	USFS/B.C.[5]
	Tree species		American Chestnut	American Chestnut	Sitka spruce	European elm	Western white pine
	Pest/pathogen		Chestnut blight	Chestnut blight	White pine weevil	Dutch Elm Disease	White pine blister rust
1	Rationale for programme	Timber value	▨	▨	■	□	■
		Cultural value	■	■	□	▨	▨
		Ecosystem functioning	■	▨	□	□	▨
		Aesthetic	□	□	□	■	□
		Returns from selling resistant material	□	□	□	▨	□
2	Screening for resistance	Field surveys	▨	▨	▨	▨	▨
		Planting trials	■	■	■	■	■
		Artificial inoculation	■	■	■	■	■
3	Tree breeding	Intraspecific tree breeding	□	■	■	□	■
		Hybridisation	■	□	□	■	□
		Genetic engineering	▨	□	□	□	□
4	Large-scale production	Seed orchards from breeding programme	■	■	■	■	■
		Seed orchards from field material	□	□	■	□	▨
5	Deployment	Co-ordination by government	▨	□	■	□	■
		Co-ordination by NGO	■	■	□	□	□
		Carried out by forestry sector	□	□	■	□	■
		Carried out by volunteers/NGO	■	■	□	▨	□
		Dependent on market demand	□	□	□	■	□
		Spatial targeting	▨	□	■	□	■
		Use of silviculture	□	□	■	□	■
6	Monitoring	Breeding or production populations	■	■	■	□	■
		Operational plantings	N/A	N/A	▨	N/A	■
	Problems	Land availability	▨	□	□	□	■
		Loss of resistance	□	□	□	▨	□
		Other threats	▨	□	□	□	□
		Developing resistant material	□	■	□	■	□

[1] The American Chestnut Foundation (TACF)

[2] The American Chestnut Co-operators Foundation (ACCF)

[3] British Columbia (B.C.) Ministry of Forests

[4] The Italian Institute of Plant Protection (IPP)

[5] Several North American programmes, involving the US Forest Service (USFS) and B.C. Ministry of Forests

from hybrids and to ensure a genetically diverse population—trees from this additional breeding are predicted to be available for operational planting between 2030 and 2050 (Westbrook 2018). Other breeding programmes also aim to identify and include trees that encompass several mechanisms of resistance and are genetically distinct from each other. For example, several forms of WPBR resistance have been documented in WWP (e.g. few infection spots, cankers absent or slower-growing, shed of infected needles; King et al. 2010). Combining these apparently distinct

Table 4   Context, objectives and timescales for resistant tree programmes. [N] (native), [NN] (Non-native), USFS (US Forest Service), IETIC (Inland Empire Tree Improvement Co-operative)

		Organisation				
		The American Chestnut Foundation (TACF)	American Chestnut Co-operators Foundation (ACCF)	B.C. Ministry of Forests	Italian Institute of Plant Protection	Several North American programmes[3]
Context and objectives	Region	North America		North America	Europe	North America
	Tree	American chestnut		Sitka spruce	Several species of elm	Western White Pine
	Threat	Chestnut blight[NN]		White pine weevil[N]	Dutch Elm Disease[NN]	White Pine Blister Rust[NN]
	Severity	Very high		High	Very high	High
	Impacts	Cultural value; Biodiversity; Forest structure and functioning; Commercial use		Timber production	Aesthetic; Costs to remove dead and diseased trees	Timber production; Disease control costs; Forest ecology
	Organisation	Not-for-profit	Not-for-profit	Government	Research institute	Government (+ industry and universities for IETIC)
	Objectives	- Species restoration for cultural, environmental, economic and biological values; - Raising awareness	- Restoration of pure-bred American chestnut particularly for cultural and environmental value; - Raising awareness	- Produce resistant Sitka spruce for economic value	- Restoration, particularly for urban and landscaping uses	- Primarily for economic value, but also ecological and environmental benefit
Timescales and costs	Start date	1983[1]	1980[1]	Provenance trial in 1974. Screening trials from 1984	Late 1970s[2]	Several programmes, beginning in 1950s and 1960s
	Investment	- $2.7 million in 2015; - USFS tests cost $1200–12,000 ha^{-1} (establishment) and $1200–2400 ha^{-1} year^{-1} (maintenance)	?	?	?	- Total IETIC costs $4.1m (1978–2006). Cost $236,459 in 2005, but also some income from seed sale (IETIC 2007)
	Status	- Resistant seed produced in several orchards; - Ongoing tests to confirm resistance; - Intend general distribution in a few years	- Ongoing breeding and testing of the most resistant material; - Putatively resistant material now supplied to volunteers for planting	- Large-scale deployment of material from breeding programmes; - Guidelines for planting resistant material	- Five patented cultivars released to market (1997–2011); - Ongoing breeding to improve resistance and viability against other threats	- Partially resistant material planted operationally over substantial areas; - Ongoing testing and breeding

? indicates that information could not be obtained from the literature consulted

[1] Incorporates previous knowledge of field resistance and material produced during earlier programmes by Connecticut Agricultural Experimentation Station and USFS

[2] Builds on material produced in earlier resistant elm programmes, particularly in the Netherlands

[3] Several semi-independent programmes in different regions of USA and Canada employing similar approaches

Table 5 Approaches used in resistant tree breeding programmes

	Organisation				
	The American Chestnut Foundation (TACF)	American Chestnut Co-operators Foundation (ACCF)	B.C. Ministry of Forests	Italian Institute of Plant Protection (IPP)	Several North American programmes
Screening	- Inoculate following a standard method and monitor trees in TACF orchards - USFS field testing of 12,000 TACF seedlings	- Inoculate following a standard method and monitor external plantings using volunteer growers	- Screening at 22 sites, with susceptible trees as controls. Weevil numbers augmented and standardised between sites - Investigate heritability of resistance and geographic differences in susceptibility	- Inoculate and screen trees in orchards - > 50,000 hybrid seedlings raised and tested for DED-resistance and other desirable traits (e.g. growth form, colour)	- Field-collected disease-free material as the basis for initial screening trials - Growth and mortality monitored after artificial inoculation - Potential resistance validated in field trials
Tree breeding	- Interspecific hybridisation with Chinese chestnut - Backcrossing, incorporating locally adapted material - Considering potential for genetic engineering - Heritability estimates of 0.2–0.5 (Steiner et al. 2017; Westbrook 2018)	- Intraspecific tree breeding, including grafts and crosses of survivors collected in the 1970s and between apparently resistance offspring - Open-pollinated trees from many locations planted and crossed	- Intraspecific tree breeding, with material from Sitka spruce range - Grafts and controlled crossing of putatively resistant trees - Heritability of 0.5 (family) and 0.9 (individual) (Alfaro et al. 2013)	- Interspecific hybridisation between European and Asian elm species - Including several provenances to maintain genetic variation	- Intraspecific tree breeding, including grafting and controlled crosses - Incorporate several mechanisms to increase durability of resistance - Heritability estimates of 0.2–0.6 depending on trait (Mahalovich 2010)
Production	- Local TACF state chapters plant centrally produced material in seed orchards - 52,000 partially resistant seedlings planted in 2015 (TACF 2015)	- Main seed orchard owned and managed by ACCF - Approx. 4000 nuts from open pollination supplied annually to volunteers providing $20 and agreeing to monitor performance	- Seed orchards owned by B.C. Ministry of Forests - Collection from geographic 'resistance zones' identified in screening	- IPP seed orchards - Commercial nurseries receiving IPP licence	- Several seed orchards, often building on previous screening and breeding - Orchards include wild-collected material, stock from earlier orchards, and more advanced material from ongoing breeding
Deployment (Scale)	- Not yet taking place (but see 'Screening' and 'Production' for an indication of scale)	- 10, 20 or 100 putatively resistant chestnuts provided annually to volunteers for test planting - Aim to plant around 4000 chestnuts annually	- B+ material (from zones with a high proportion of resistance) from 1990s - Breeding programme seed (Class A) available - >400,000 trees planted from 2005 to 2011	- Available commercially from licenced nurseries - Planting for conservation purposes being trialled	- Large area potentially of interest (to reverse historical losses) - Seed available for planting, but deployment limited by land availability
Deployment (Strategy)	- Likely to target environmentally suitable sites and include silviculture to increase chance of success - Likely to involve volunteers - Aim to deploy a population of trees able to persist as a genetically diverse wild species, likely based on seed orchard seedlings	- Currently, nuts provided to volunteers contributing $20 to ACCF (material is open pollinated with only a proportion expected to have partial resistance) - Will probably use seed orchard seedlings	- Recommend up to 30–50% stocking where weevil hazard is medium–high - Uses seed orchard seedlings	- Scale and locations of operational deployment not clear - Several clones available, but planting large numbers of a single clone is not recommended	- Seed orchard seedlings distributed to public and private forestry organisations - Recommended for operational use in areas with medium–high WPBR hazard - May be unsuitable in highest hazard zones, with more virulent rust strains - Avoid in pure stands
Monitoring	- Field testing of ongoing trials by USFS - Data from TACF breeding and production orchards	- Volunteer growers provide annual performance data	- Primarily within long-term screening trials	- Some monitoring by organisations that plant IPP material	- Within field populations and breeding and production orchards - Also includes susceptible trees as controls

Table 5 (continued)

	The American Chestnut Foundation (TACF)	American Chestnut Co-operators Foundation (ACCF)	B.C. Ministry of Forests	Italian Institute of Plant Protection (IPP)	Several North American programmes
Organisation					
Problems	- Emphasise need to record field performance - Land availability for seed orchards and deployment - Mortality from other causes (e.g. Phytophthora) ranges from 12 to 70% - Too soon to assess durability of resistance	- Resistance in American chestnut is partial, occurs at very low frequency, and has low heritability - Initial problems gathering data on performance	- Resistance is partial, so not recommended for deployment at high densities in weevil hazard areas	- Some resistant cultivars withdrawn from sale due to susceptibility to other pests and pathogens - Demand and confidence also potentially affected by losses of putatively resistant elms from other breeding programmes	- Mechanism of complete resistance has been overcome in some areas - Partial resistance mechanism more durable, but some impacts occur - Land availability for planting
Other strategies used	- Silviculture - Targeted deployment to suitable sites	- Silviculture - Targeted deployment to suitable sites - Hypovirulent blight to reduce impacts	- Resistant trees viewed as the most effective approach for using Sitka spruce in pine weevil areas	- N/A	- Resistant trees viewed as a key part of strategies to recover species - Silviculture to maintain regeneration - Removal/pruning of affected trees

mechanisms is hoped to reduce the risk that WPBR subsequently overcomes host resistance, whilst ensuring a broad genetic base that can maintain the capacity to adapt to other environmental pressures (Hunt 2004; Mahalovich 2010; Fig. 5).

3.4 Large-scale production

Seed orchards are established to produce resistant material for planting. All of the case studies used material from the breeding programme, although seed from regions identified as having a high proportion of resistance can be an interim measure (e.g. Alfaro et al. 2013). Orchards are often on a substantial scale, and therefore require stable funding commitments and co-ordination. In some cases, this is available through existing government forestry infrastructure (e.g. Alfaro et al. 2013). Equally, organisations such as TACF have used extensive communication and outreach to develop a network of volunteer chapters, resulting in many additional seed orchards that complement the central TACF facility (Fitzsimmons et al. 2014; TACF 2015).

3.5 Planting resistant material—who and how?

Of the case studies investigated, the Sitka spruce-pine weevil and the WWP-WPBR programmes have both deployed material operationally (Figs. 3 and 5). These programmes have involved long-term government investment and research and are well-suited to centrally co-ordinated planting, which is carried out by government and by private forestry. Notably, partially resistant B+ Sitka spruce from regions identified as having high levels of resistance was used as a low-cost interim deployment measure from the 1990s (Fig. 3), with more fully resistant (Class A) material subsequently planted as the breeding and production programme became established (Alfaro et al. 2013). Outputs from TACF and ACCF American chestnut breeding are subject to ongoing testing, and future deployment may involve working extensively with volunteers (Fitzsimmons et al. 2014). The IPP appears to focus more on the development of resistant elms (rather than large-scale deployment), meaning that this programme is perhaps more reliant on other organisations devising and implementing deployment strategies independently.

Planting strategies often recommend avoiding using monocultures or large blocks of genetically similar individuals, and limiting planting density in zones at high risk from the pest or pathogen (King et al. 2010; Alfaro et al. 2013; Sniezko et al. 2014; Table 3). For example, guidance from Natural Resources Canada advises that if resistant Sitka spruce is planted in high pine weevil hazard zones, a range of genotypes should be used and mixed with other species (https://cfs.nrcan.gc.ca/projects/106; Alfaro et al. 2013). Similarly, planting several WWP genotypes with distinct

resistance mechanisms is suggested to mitigate the risk from WPBR strains overcoming resistance (Mahalovich 2010; Schwandt et al. 2010; Sniezko et al. 2014), whilst mixing with other native tree species can provide some insurance against losses in zones with high rust hazard (Schwandt et al. 2013). These practices reflect views that monocultures experience greater impacts from species-specific threats than mixed forests, and that genetically similar stands are vulnerable to variants of the pest or pathogen and to changing environmental conditions (Fins et al. 2001; Heppner and Turner 2006; Alfaro et al. 2013; Jacobs et al. 2013). Targeted planting to achieve specific benefits is also sometimes used (e.g. Butterfly Conservation trials of DED-resistant elms to support the conservation of rare butterflies; Brookes 2014). Lastly, silvicultural interventions such as the removal of competitors, pruning to remove or prevent infection, and the use of deer exclosures are important in some programmes (Schwandt et al. 2010; Jacobs et al. 2013; Schwandt et al. 2013) but may be less effective in others (King and Alfaro 2009).

3.6 Monitoring

Understanding what happens to resistant trees after planting is important for two reasons (Kearns et al. 2012; Schwandt et al. 2013). Firstly, it increases the chance that any loss of resistance will be detected at an early stage, thereby informing future tree breeding efforts and mitigation measures such as containment. Secondly, it allows the performance of resistant material against other biotic and abiotic pressures to be evaluated. Monitoring to understand general performance is likely to be short to medium-term (i.e. sufficient to represent the range of threats typically experienced by trees). In principle, the breakdown of host resistance could occur at any stage, due to evolution of the local pest/pathogen population or to accidental introduction of a new strain. As such, monitoring for this purpose is perhaps more open-ended, although the regularity and intensity might decline over time if evidence mounts that resistance is durable. The Sitka spruce screening trials from the 1970s onward provide good evidence that weevil attack rates in putatively resistant material are consistently lower than for non-resistant trees over a period encompassing multiple outbreaks and a range of environmental stresses (King and Alfaro 2009). Similar information is available for WWP, with data on infection and mortality rates for several plantings aged 10–30 years indicating variation in performance across sites and depending on the mechanism of resistance (Fins et al. 2001; Schwandt et al. 2013).

Monitoring data for field plantings is shorter-term in the other case studies considered. TACF are testing the viability of material from later stages of the breeding programme by monitoring large-scale field trials established in collaboration with the US Forest Service: although these trials began in 2009, valuable data have already been collected on the extent and causes of mortality (Clark et al. 2014). Volunteer growers for ACCF also agree to supply annual reports on the performance of planted chestnuts, whilst the field trials conducted by Butterfly Conservation provide useful information on the performance of IPP elms and several other cultivars (Brookes 2014).

4 Discussion

4.1 Successes and problems

The case studies illustrate that the difficulty of developing resistance can differ markedly between pest-pathogen systems (e.g. depending on the heritability and frequency of resistance in the population), and represents an important constraint in some cases. The long-term viability of resistant trees may also be compromised by three broad threats: (i) the emergence of pest/pathogen strains that overcome resistance, (ii) impacts from the target pest or pathogen if resistance is partial, and (iii) impacts from other current or emerging environmental pressures (e.g. other pests or pathogens, abiotic stresses). These problems have affected resistant tree programmes differently. New strains of WPBR and DED have been highly damaging to some previously resistant WWP and to elms, and impacts on partially resistant WWP trees can occur (Kearns et al. 2012). Trees resistant to specific threats can also be affected by other environmental pressures—e.g. the DED-resistant 'Morfeo' elm was withdrawn from UK nurseries due to the particular susceptibility of this clone to the pathogen elm yellows (https://www.ashridgetrees.co.uk/morfeo-elm-tree-for-sale, accessed March 72,017; Mittempergher and Santini 2004; Brookes 2014), whilst *Phytophthora* and deer are the main causes of mortality in trials of blight-resistant American chestnut (Clark et al. 2014). Equally, the Sitka spruce and WWP programmes appear relatively successful, with substantial numbers of resistant trees planted operationally, evidence for viability, and indications that resistant trees may be an effective strategy (Alfaro et al. 2013; Sniezko and Koch 2017). The comparative success of these programmes is probably also a consequence of the level of resistance to pine weevil and WPBR within the respective natural populations (in contrast with the elm and American chestnut examples).

Understanding the demand for resistant trees is a second important consideration. In some cases, scepticism arising from previous failures (and replacement costs) of trees marketed as resistant has reduced demand (Buiteveld et al. 2015). In others, demand may relate more to how the resistant material is produced or performs. For example, DED-resistant elms also need to replicate the aesthetic qualities of the

affected species, whilst resistant trees of primarily commercial species must maintain timber yields. Where public support or involvement is important (e.g. reliance on volunteers, use of public lands), potentially contentious approaches to developing or deploying resistant trees such as genetic modification or extensive vegetation clearance and silviculture to promote establishment of resistant material should also be very carefully evaluated.

If resistant trees are developed, suitable sites to establish seed orchards and plant material are still needed. Land availability can therefore be an impediment, particularly where restoration is involved and the affected species has been displaced by other trees (Fitzsimmons et al. 2014). Indeed, some have argued that re-establishing species such as WWP extensively will require the potentially controversial clearance of large areas of vegetation, alongside silviculture to promote the regeneration and spread of resistant trees (Fins et al. 2001; Schwandt et al. 2010).

4.2 Timescales and costs

The case studies suggest at least 10–20 years are required before operational planting of resistant material (Figs. 1, 2, 3, 4 and 5), which itself can be protracted (Schwandt et al. 2010). Newer programmes could be expedited by technological improvements (e.g. genomic methods for screening and breeding; Steiner et al. 2017) and by planting partially resistant material as an interim measure (Alfaro et al. 2013), but even under optimal circumstances resistant tree programmes appear to be

a medium-term strategy, with many not yet reaching the stage of field planting (Figs. 1, 2, 3, 4 and 5; Table 1, see also http://www.fao.org/forestry/26462/en/). Timescales also reflect the emphasis placed on testing and breeding (to demonstrate viability) compared with the pressure to move rapidly to large-scale planting (to mitigate impacts). These priorities can be pursued simultaneously to an extent, but the balance is influenced by several factors—e.g. willingness of stakeholders to take risks, urgency of the threat, potential benefits from resistant trees, consequences of unanticipated damage and mortality. For example, there appears to be a willingness to make use of resistant Sitka spruce and WWP, perhaps reflecting the potential benefits to forestry, general confidence that the material is viable, and an assessment that some losses due to partial resistance are still acceptable. Lastly, timescales sometimes reflect the need to meet objectives beyond producing trees that are resistant to a specific threat, such as incorporating other desirable traits, maintaining genetic variation, or using particular tree breeding approaches that ensure the results meet the objectives of the programme (e.g. backcrossing by TACF).

The investment in resistant tree programmes was not always clear in the available literature, although as an indication the US Forest Service spent an estimated $6.9 million on American chestnut restoration research from 2003 to 2013 (Clark et al. 2014), whilst TACF accounts have annual expenditure of $2–3 million (TACF 2015). TACF costs are not necessarily representative because of the broad scope of the work (large-scale restoration, a complex tree breeding programme, and substantial public outreach). Indeed, the only other case
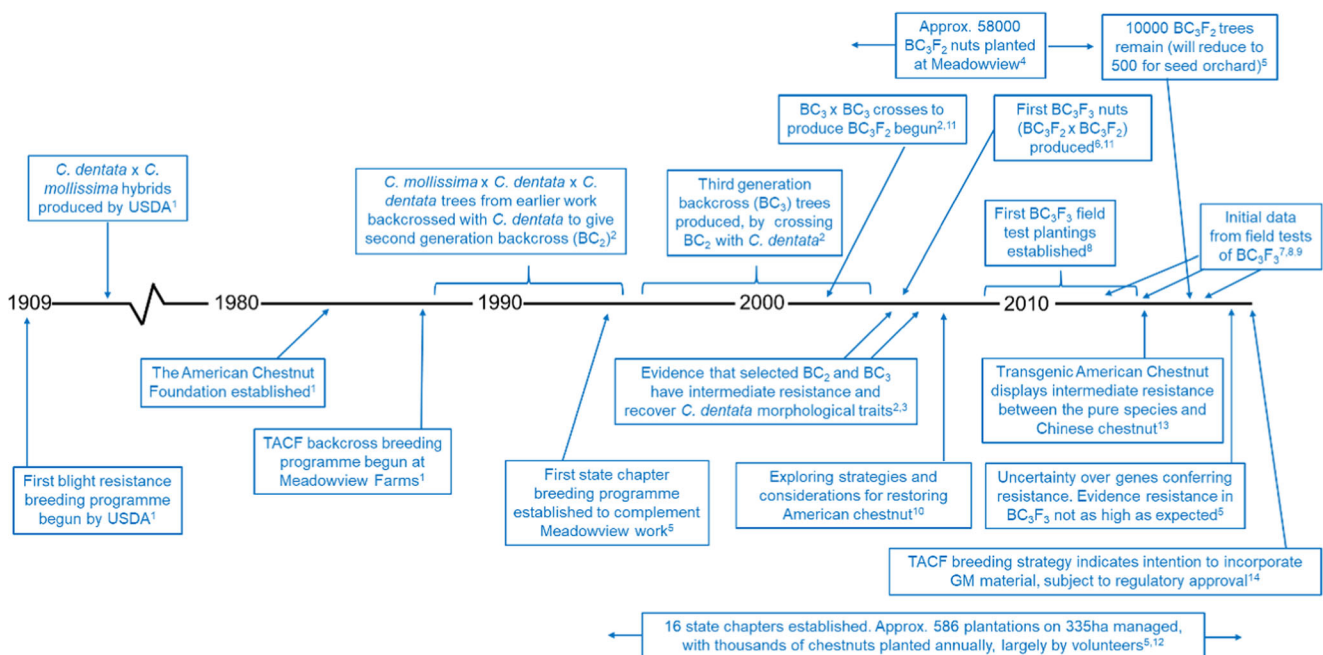

Fig. 1 Timeline indicating prominent events in American chestnut (*Castanea dentata*) resistance programme carried out by The American Chestnut Foundation (TACF). Numbered references are: [1]Jacobs et al. (2013). [2]Hebard (2005b). [3]Diskin et al. (2006). [4]Hebard (2012).

[5]Steiner et al. (2017). [6]Hebard (2005a). [7]Clark et al. (2011). [8]Clark et al. (2014). [9]Clark et al. (2016). [10]Jacobs (2007). [11]TACF Annual Report (2014). [12]TACF Annual Report (2016). [13]Newhouse et al. (2014). [14]Westbrook (2018)
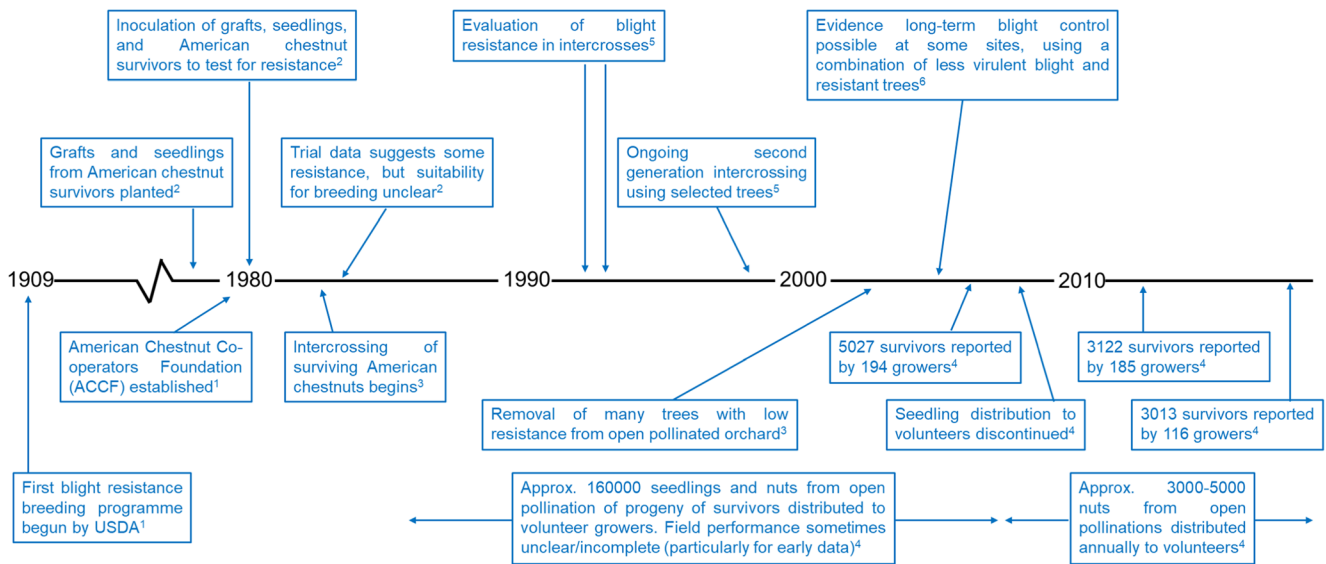
Fig. 2 Timeline indicating prominent events in American chestnut (*Castanea dentata*) breeding programme carried out by the American Chestnut Co-operators Foundation (ACCF). Numbered references are: [1]Jacobs et al. (2013). [2]Griffin et al. (1983). [3]http://www.accf-online.org/ accf1.htm. [4]http://www.accf-online.org/breed.html. [5]ACCF Newsletters (2002–2017; http://www.accf-online.org/news.html). [6]Griffin et al. (2005)

for which we found clear cost estimates was the WWP-WPBR programme carried out by the Inland Empire Tree Improvement Co-operative (IETIC), which reported a total cost of $4.1 million from 1978 to 2006 and a cost of $236,459 in 2005 (IETIC 2007). Although it is difficult to generalise on costs beyond emphasising that the screening, breeding and production stages of resistant tree programmes require sustained funding, these two examples give some indication of the potential range and duration of investment. It is also notable that seed sales and other activities provided some

income for IETIC: the former was variable but returned $40–50,000 in some years (IETIC 2007). Sources of financial support reflect the differing aims of resistant tree programmes, and include donations, grants, and volunteer time (TACF, ACCF) and government funding (Sitka spruce, WWP). An evaluation of the potential costs, benefits (including non-economic values), funding sources and alternative mitigation measures at an early stage could help to inform decisions over whether a proposed resistant tree programme is likely to be an effective option.
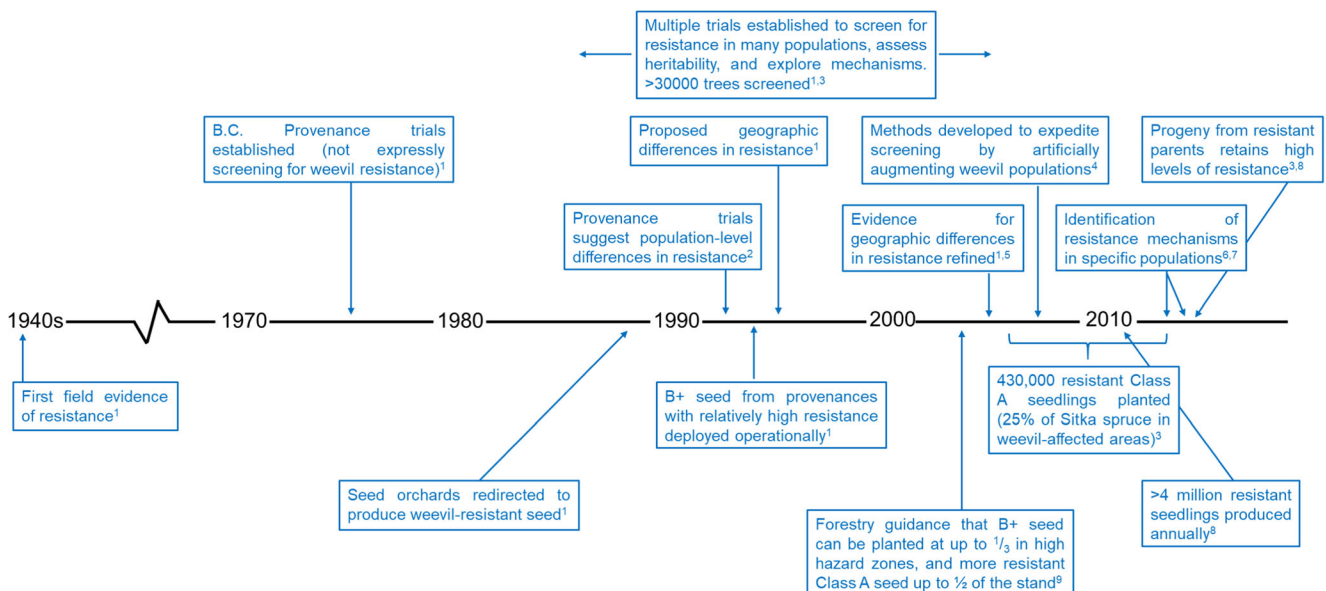
Fig. 3 Timeline indicating prominent events in the Sitka spruce (*Picea sitchensis*) breeding programme carried out by the British Columbia (B.C.) Ministry of Forests. Numbered references are: [1]King and Alfaro (2009). [2]Ying (1991). [3]Alfaro et al. (2013). [4]Alfaro et al. (2008). [5]King et al. (2004). [6]King et al. (2011). [7]Moreira et al. (2012). [8]Alfaro and King (2012). [9]Heppner and Turner (2006)
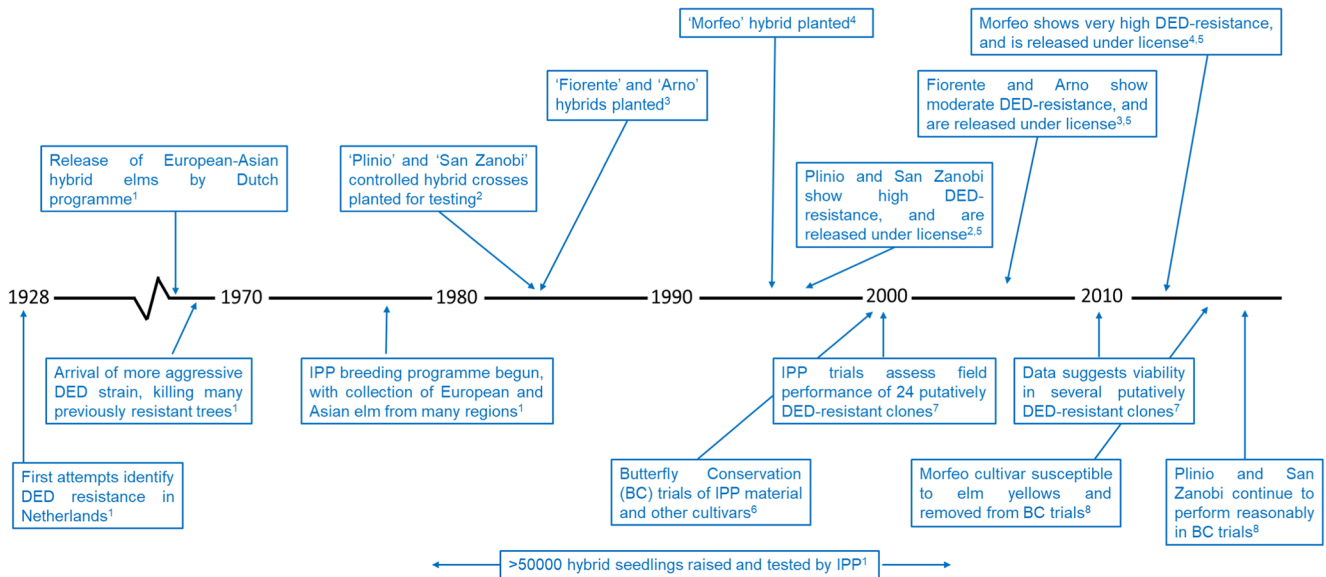
Fig. 4 Timeline indicating prominent events in the elm (*Ulnus* spp.) breeding programme carried out by the Italian Institute of Plant Protection (IPP). Numbered references are: [1]Mittempergher and Santini (2004). [2]Santini et al. (2002). [3]Santini et al. (2007). [4]Santini et al. (2011). [5]Santini et al. (2012). [6]Brookes (2010). [7]Santini et al. (2010). [8]Brookes (2014)

4.3 What makes a successful resistant tree programme?

Comparing the case studies highlights several points that may influence the success of resistant tree programmes:

- The most effective programmes have had central co-ordination and long-term commitment, e.g. by government

and/or well-funded NGOs. This arises (i) if the species has a high timber value and/or (ii) if the species (or other benefits associated with it) has a high cultural/societal value and so can generate substantial public support. If neither of these criteria are met, a lack of resources or co-ordination may lead to piecemeal or incomplete approaches, or the proliferation of putatively resistant material from different sources with little guidance on field performance and viability.
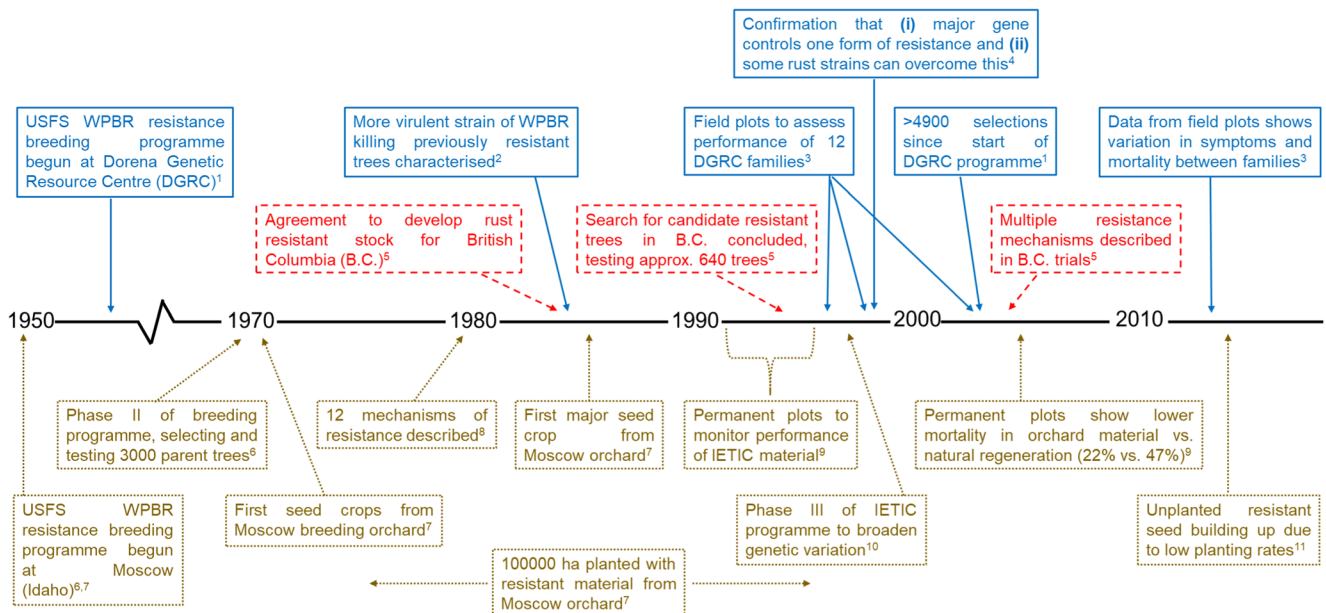
Fig. 5 Timeline indicating prominent events in Western White Pine (WWP) breeding programmes carried out in North America. Programmes shown: Dorena Genetic Resource Centre (blue text, solid lines); British Columbia Ministry of Forests (red text, dashed lines); Inland Empire Tree Improvement Co-operative (brown text, dotted lines). Numbered references are: [1]King et al. (2010). [2]McDonald et al. (1984). [3]Sniezko et al. (2012). [4]Kinloch et al. (1999). [5]Hunt (2004). [6]Bingham (1983). [7]Fins et al. (2001). [8]Hoff and McDonald (1980). [9]Kearns et al. (2012). [10]Mahalovich (2010). [11]Schwandt et al. (2013)

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- Success is influenced by the level of resistance present in individual trees, the frequency of resistance in the population, and the heritability of resistance. As such, this represents important contextual knowledge for guiding the choice of approach and the expectations.
- It is important to consider current and potential future risks to the species in addition to the target pest or pathogen—the benefits of trees resistant to a specific threat are negated if it is susceptible to other threats.
- Demand should be evaluated, and the priorities of potential supporters and end users should inform the methods used to produce resistant trees.
- Operational deployment should balance the urgency of the threat with the consequences if resistant material does not perform as hoped. The case studies presented here are responding to situations with either very extensive mortality or chronic impacts, but the urgency may differ for an emerging pest or pathogen.
- Deployment strategies should be informed by the risks of imposing a strong selection pressure on the pest or pathogen to evolve to overcome host resistance, and by potential impacts on partially resistant trees.
- Continued monitoring of field performance is important for evaluation, and can help to identify and mitigate emerging threats (e.g. new pathogen strains)

5 Conclusions

The approaches and the outcomes for resistant tree programmes are sometimes not well-documented, or may be dispersed across the grey literature (e.g. technical reports, conference proceedings, websites, management guidelines). Greater communication and accessibility of information would therefore help to better generalise on approaches, timescales and effectiveness. Nonetheless, the case studies illustrate that resistant tree programmes are medium to long-term approaches that have varying levels of success and typically require considerable investment. Expectations should reflect these realities and the challenges of the specific host-pest/pathogen system. Equally, the case studies also show that adequately resourced and well-planned resistant tree programmes can form an important part of strategies to mitigate impacts from pests and pathogens.

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

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