The potential of alternative conifers to replace larch species in Ireland, in response to the threat of *Phytophthora ramorum*

Richard Walsh[ab*], Andrew Cameron[b], Scott McG. Wilson[c] and Niall Farrelly[a]

Abstract

Forest ecosystems are facing many challenges in the wake of recent pest and disease outbreaks, coupled with uncertain future climate conditions. A particular challenge emerges from the recent outbreak of *Phytophthora ramorum* identified in Japanese larch (*Larix kaempferi*) in 2010. Its subsequent spread has caused widespread damage to Japanese larch stands and has resulted in the Japanese, European (*Larix decidua*) and hybrid (*Larix* × *eurolepis*) larches no longer being grant-aided in the Irish afforestation programme in Ireland. Over 20% of forest stands contain some quantity of larch, with a total area of 32,057 ha. Japanese larch is the predominant species with 27,859 ha, 86% occurring as mixed stands and 79% in mixture with Sitka spruce (*Picea sitchensis*). The objective of the study was to examine the range of alternative conifer species that may be suitable to replace larch which potentially have similar or higher levels of productivity, acceptable timber properties, while affording reduced levels of risk from pest/disease outbreak. To assess productivity, yield class of a range of species in mixture with larch across a gradient of soil types was assessed. Analysis of this data indicated that Sitka spruce, western red cedar (*Thuja plicata*), grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), Norway spruce (*Picea abies*), European silver fir (*Abies alba*), noble fir (*Abies procera*) and Douglas fir (*Pseudotsuga menziesii*) provide suitable alternatives, showing higher levels of productivity across a range of soil types. A strong positive correlation was found between the yield classes of (a) Japanese larch and western hemlock ($r = 0.70$), (b) hybrid larch and Douglas fir ($r = 0.73$) and (c) European larch and Sitka spruce ($r = 0.61$) growing on the same sites. Regression equations were developed between the site yields of Japanese, European and hybrid larches and those of alternative species, as a useful tool to predict growth performance of potential alternative species across a range of soil types where larch is currently growing. The predictive power varied for different species pairings (r^2 of 0.24 to 0.87) with the strongest relationships between the yields of Japanese larch and Norway spruce on basin peat ($r^2 = 0.71$) and Japanese larch and Douglas fir on podzol soils ($r^2 = 0.76$; $y = 1.2632x + 2.6316$). Given the significance of Sitka spruce/Japanese larch mixtures in Irish forestry, future research should focus on the potential for mixtures combining Sitka spruce and alternative

[a] Teagasc, Mellows Centre, Athenry, Co. Galway.
[b] Institute of Biological and Environmental Sciences, University of Aberdeen, St. Machar Drive, Aberdeen AB22 3UU, Scotland.
[c] 3 Thorngrove Crescent, Aberdeen, AB15 7FH, Scotland.
[*] Corresponding author: richard.t.walsh@teagasc.ie

Pacific conifers (e.g. Douglas fir, grand fir, western hemlock and western red cedar) that may enhance the resilience of and maintain productivity.

Keywords: *Larch,* Phytophthora ramorum*, pests and diseases, alternative conifers, silvicultural mixtures, forest yield.*

Introduction

Over the past decade, there has been a rise in the number of damaging invasive biotic agents detected in European (Jones and Baker 2007, Brasier 2008) and Irish forests (McCracken 2013, O'Hanlon et al. 2016a). Some of the potential contributing factors leading to this increase include disturbances to forest ecosystems by humans, changing climatic conditions, increases in international trade (Stenlid et al. 2011) and international travel by humans (Hulme 2009), with the spread of pathogens possibly having been facilitated by transportation of infected plant material to new areas (Levine and D'Antonio 2003). More recently, climate change has potentially reduced the abiotic constraints that formerly prevented the geographical spread of damaging pathogens (Pautasso et al. 2010). The rise in biotic risk has consequentially reduced the range of tree species available for afforestation and reforestation, with foresters increasingly dependent on a few species for establishment of commercial plantations (Read et al. 2009).

The recent outbreaks of *Phytophthora ramorum* (Werres, De Cock & Man in't Veld) in *Larix* spp. and ash dieback disease (*Hymenoscyphus fraxineus*) in *Fraxinus* spp. in Ireland have highlighted the risks to our forest resources from pathogenic attacks, and both diseases have caused considerable damage to forests in Ireland and Britain (Brasier and Webber 2010, Webber et al. 2010). The fungal pathogen *Phytophthora ramorum* was first detected in Ireland on *Rhododendron* spp. (EPPO 2003, O'Hanlon et al. 2016b) and was subsequently detected on Japanese larch (*Larix kaempferi* (Lamb.) Carr.) in 2010 (EPPO 2010). This multi-lineage oomycete pathogen (O'Hanlon et al. 2017) has now been detected on 30 hosts in Ireland, among which the coniferous genera include *Abies*, *Larix* and *Picea* (O'Hanlon et al. 2016b). Larches (including Japanese, hybrid (*Larix* × *eurolepis* A. Henry) and European (*Larix decidua* Mill.) larch) appear to display the least resistance. It is an aggressive and unpredictable pathogen and is a serious threat to Irish forestry (O'Hanlon et al. 2014).

More recently, red band needle blight (*Dothistroma septosporum* Dorog.) has been detected in young Scots pine (*Pinus sylvestris* L.) growing in Ireland (Cathal Ryan, Forest Service, pers. comm.). This disease has previously caused widespread dieback and mortality in other *Pinus* species including Corsican pine (*Pinus nigra* subsp. *laricio* Maire) in England and Wales, and lodgepole pine (*Pinus contorta* Douglas ex Loudon) in Scotland (Cameron 2015). The lesser known *Phytophthora lateralis* has been reported causing death in Lawson cypress (*Chamaecyparis lawsoniana* (A.Murray bis) Parl.) in Ireland (O'Hanlon et al. 2016a) and also has infected this species and, occasionally, western red cedar (*Thuja plicata* Donn ex D.Don) in Britain (Green and Webber 2015).

Larch species are among the more important commercial conifer tree species in Irish forestry. The extensive use of larch in Irish forests is explained by the relative ease of plantation establishment, satisfactory productivity and durable, versatile timber, marketable in Britain and Ireland. Larch also provides an important role in biodiversity, permitting the retention of ground vegetation below the canopy, enhancing the support of macrofungi on the forest floor (Heslin et al. 1992), enhancing recreational amenity and improving the visual appeal of forest landscapes through the contrast of colour in winter foliage. These species have found favour in mixed species stands where they are commonly used as the second or third species, occupying a minority of the canopy. They were used extensively in the afforestation programme in Ireland up to 2010, typically in mixture with Sitka spruce (*Picea sitchensis* (Bong.) Carr.) at a rate of 80% spruce to 20% larch, often utilised in Ireland and Britain to provide a level of species diversity in Sitka spruce stands (Mason 2014). *P. ramorum* poses a significant threat to the standing resource of larch and is likely to have economic implications for a range of end-use markets, including those for fencing and exterior cladding (Brasier and Webber 2010). The extensive damage to larch caused by *P. ramorum* in both Ireland and Britain indicates the potential for invasive damaging pathogens to undermine future forest plantations, including a reduction in the range of tree species available for commercial use. While the current afforestation programme in Ireland lists a range of coniferous and broadleaved species that remain eligible for grant aid, species choice is becoming more restricted with the withdrawal of larch, ash (*Fraxinus excelsior* L.) and Lawson cypress from the permitted list of species (DAFM 2016). As a result of this reduction in species choice and the need to replace stands of diseased larch trees, an initial review was undertaken to explore the potential of alternative conifer species that have potentially similar or increased levels of productivity, acceptable timber properties, while affording reduced levels of biotic risk. Therefore, the objective of the study was to examine the range of alternative conifer species that may be suitable to replace larch in both restocking and new afforestation schemes.

Materials and methods

An estimate of the area of larch in Ireland that may be susceptible to disease threat was obtained through an examination of inventory databases for privately owned forests (provided by the Forest Service, Department of Agriculture, Food and Marine) and for state owned forests (provided by inventory branch of Coillte, the state forestry agency). Stands containing Japanese larch (149,837 ha), hybrid larch (12,964 ha) and European larch (5,777 ha) amount to a gross area of 165,362 ha, and 3,093 ha stands contain multiple larch species (Figure 1). Of the stand area containing larch, 56% (93,048 ha) was classified as being in private ownership and 44% (72,314 ha) owned by Coillte. Initially, all sub-compartments were selected in both databases containing larch species either in pure or mixed stands. For mixed species stands, the area occupied by each species was assessed by multiplying the stand area by the proportion of the canopy cover represented by each species. Stand details (e.g. ownership, age, canopy cover, yield class[1]) and site parameters (elevation, mean annual temperature, degree days and average wind speed) were derived from a digital elevation model and spatial climatic data (Met Eireann 2017, Sweeney and Fealy 2003) processed within a Geographic Information System (GIS). The soil type for each stand including larch species was identified using a digitised version of the General Soil Map of Ireland (Gardiner and Radford 1980) (Table 1).

Identifying potential alternative conifer species to replace larch requires an evaluation of the growth performance (yield class) of companion conifer species across a range of soil types. Suitable alternative species should show similar or higher levels of productivity on equivalent sites, and should represent a lower level of biotic risk, hence those species most at risk from existing invasive pathogens were excluded (e.g. Lawson cypress as susceptible to *Phytophthora* spp. and pines as susceptible to *Dothistroma* spp., respectively).

Relationships were examined between the productivity of Japanese larch and, where relevant, hybrid and European larch, and the alternative conifer species growing within the same stands (and it is thereby inferred under similar climate and soil conditions). The analysis were restricted to those mixed larch stands where larch canopy cover exceeded 20% (to minimise early growth competition effects). Finally, where productivity data were available, linear regressions between the productivity of Japanese larch and of alternative conifers (e.g. Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Douglas ex D.Don) Lindl.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar growing on the same sites) were used to develop equations to predict the potential yield class of those alternative conifer species based on the measured yield of Japanese larch on a given site.

[1] Yield class is an index of potential productivity of stands, based on a relationship between stand dominant height and age (Edwards and Christie 1981). In the inventory, procedure for measurement is to take the top height of the largest diameter at breast height tree within a 100 m^2 (200 m^2 in mixture) plot within the stand, with number plots increasing with sub-compartment area and number of species in mixture (minimum of 4 plots).

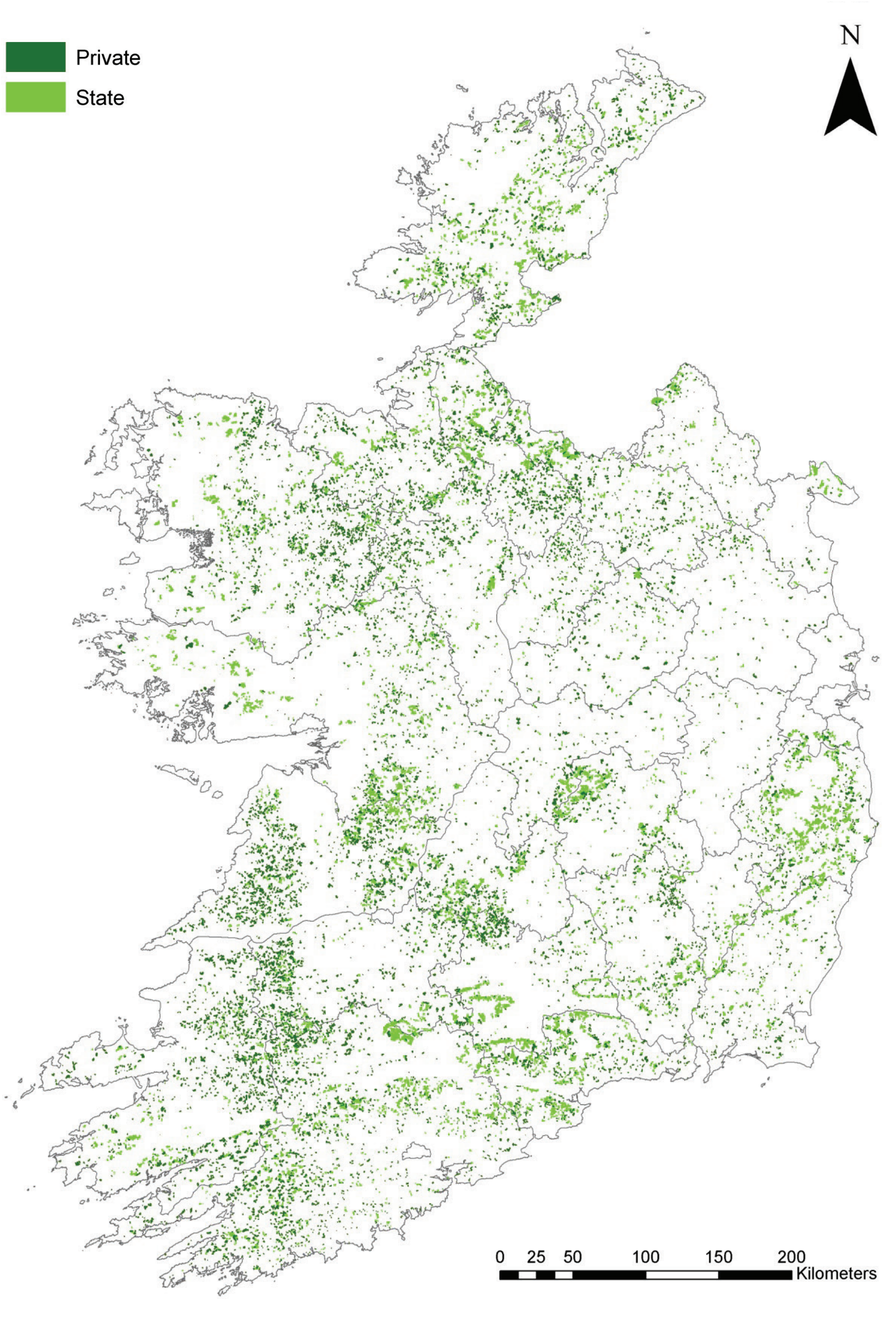

Figure 1: *Distribution of stands in the Republic of Ireland containing larch species under threat from* P. ramorum *distinguished by public and private ownership*.

Table 1: *Site characteristics including elevation (m), total area (ha) and average yield class (YC; m^3 ha^{-1} yr^{-1}) of areas planted with larch species classified by principle soil type.*

Soil[a]	Elevation[b]		Total area	*Japanese larch*				*Hybrid larch*				*European larch*			
				Pure		Mixed		Pure		Mixed		Pure		Mixed	
				Area	YC	Area	YC	Area	YC	Area	YC	Area	YC	Area	YC
ABE	104	(0-315)	2,025.8	252.7	10.2	1,264.5	11.3	98.6	12.4	220.6	12.3	35.0	7.3	154.6	7.5
BaP	72	(1-84)	1,348.5	41.3	11.8	1,146.5	10.6	11.1	7.6	96.2	11.2	11.7	6.0	41.6	7.7
BlP	183	(1-546)	4,998.3	624.4	8.8	4,062.0	9.5	18.3	11.5	233.7	10.2	15.3	8.0	44.6	7.2
BrP	176	(0-542)	5,735.6	944.2	10.2	3,911.9	10.5	169.7	11.3	506.2	11.5	36.6	7.1	167.1	7.3
G	123	(0-493)	8,476.6	739.4	10.0	6,731.9	10.8	84.4	10.9	659.8	11.4	82.2	8.0	178.8	7.3
GBP	88	(0-305)	2,775.5	170.4	11.0	1,949.6	10.5	48.1	11.7	201.2	11.2	137.3	8.0	268.9	7.4
L	163	(0-519)	542.7	83.3	8.4	422.8	9.8	6.8	10.0	22.8	9.3	1.4	6.0	5.4	5.6
PG	250	(85-421)	526.1	63.1	9.8	426.6	10.6	5.1	-	11.5	11.3	8.7	7.3	11.2	7.0
PP	220	(0-548)	4,176.4	718.4	9.4	3,070.7	9.9	45.2	10.3	182.0	10.7	43.9	7.0	116.1	7.1
P	175	(13-419)	986.2	116.0	10.3	669.3	10.4	15.1	11.2	79.8	11.4	4.3	8.0	51.8	7.2
R	167	(14-279)	49.1	3.7	9.0	35.6	9.1	0.6	-	0.3	-	1.0	-	7.9	6.8
SBE	53	(7-200)	362.5	84.2	8.6	224.6	9.3	1.0	12.0	31.7	11.5	7.8	6.0	13.1	7.1
OS	141	(0-253)	54.3	5.0	6.0	46.7	11.1	-	-	2.1	14.0	-	-	0.5	4.0
Total			**32,057.5**	**3,896.2**		**23,962.7**		**504.0**		**2,248.1**		**385.0**		**1,061.4**	

[a] Where ABE is acid brown earth, BaP is basin peat, BlP is blanket peat, Brp is brown podzolic, G is gley, GBP is grey brown podzolic, L is lithosol, PG is peaty gley, PP is peaty podzol, P is podzol, R is rendzina, SBE is shallow brown earth and OS is other soils.

[b] The range in elevation is included in brackets.

Results

The majority of the larch stock in Ireland (27,272 ha) occurs in mixed species stands and a smaller amount (4,785 ha) in pure larch stands (Table 1). The area occupied by hybrid larch (2,487 ha) and European larch (1,268 ha) is much lower than the area represented by Japanese larch (27,859 ha). Larch species have been planted over a wide range of site and soil conditions in Ireland. They are all found at elevations between sea level and 548 m a.s.l. for Japanese larch, to 447 m for hybrid larch and to 457 m for European larch; in low and high rainfall areas (Japanese larch from 692 to 3,022 mm, hybrid larch from 740 to 2,807 mm and European larch from 700 to 2,730 mm). In Ireland, larch species are subject to shorter and longer growing seasons with ranging degree days[2] for Japanese larch (534 to 2,149), hybrid larch (774 to 2,078) and European larch (916 to 2,117) indicating a wide geographic spread. A higher percentage of pure larch stands (64%), especially older stands of European larch, occur on well drained soils (brown podzolic, podzols, acid brown earths and grey brown podzolics). Occurrence on poorly drained soils (gleys, blanket peats and basin peats) was higher for mixed stands, typically where Japanese larch has been mixed with conifer species more suited to wetter conditions (i.e. Sitka spruce and lodgepole pine). This explains the increased planting of larch on gley soils over the period 1996 to 2010, reaching a peak in 2001 (999 ha), coinciding with grant aid for establishment of Sitka spruce/Japanese larch mixtures (Figure 2). The primary soil types planted over the period 1996 – 2010 were gleys (6,760 ha), blanket and basin peats (5,339 ha) and brown podzolic soils (4,318 ha) (Figure 2). Annual planting of larch declined dramatically after 2010 because of the outbreak of *P. ramorum* and decreased to virtually zero in 2014.

Of the Japanese larch mixed stands (23,963 ha), a significant proportion occurs on gley soils (6,732 ha), and this is also reflected in the location of hybrid larch mixed (2,248 ha) stands, with 660 ha found on gleys. The area of European larch mixed stands (1,061 ha) is primarily found on free-draining brown earth and podzolic soils (269 ha). The predominant companion conifer species for all larches is Sitka spruce, accounting for 18,870 ha or 79% of the area of Japanese larch mixtures, while also amounting to 1,540 ha and 238 ha of the area for hybrid larch and European larch mixtures, respectively. Other conifer species that represent a significant area in mixture with larches are lodgepole pine, Norway spruce (*Picea abies* (L.) H. Karst.), Douglas fir and Scots pine. The productivity of Japanese larch in mixed crops (10.1 m^3 ha^{-1} yr^{-1}) was consistently greater than in pure stands 9.7 m^3 ha^{-1} yr^{-1}) across a range of elevation categories up to 550 m. The exception is where Japanese larch occurs in mixed stands with less common conifer species such as noble fir (*Abies procera* Rehder) (8.4 m^3 ha^{-1} yr^{-1}) and European silver fir (*Abies alba* Mill.) (9.5 m^3 ha^{-1} yr^{-1}) (Table 2). The average productivity of hybrid and European larch in mixed stands is

[2] Degree days are the accumulated day-degrees above 5 °C which provides a measure of total heat accumulation.

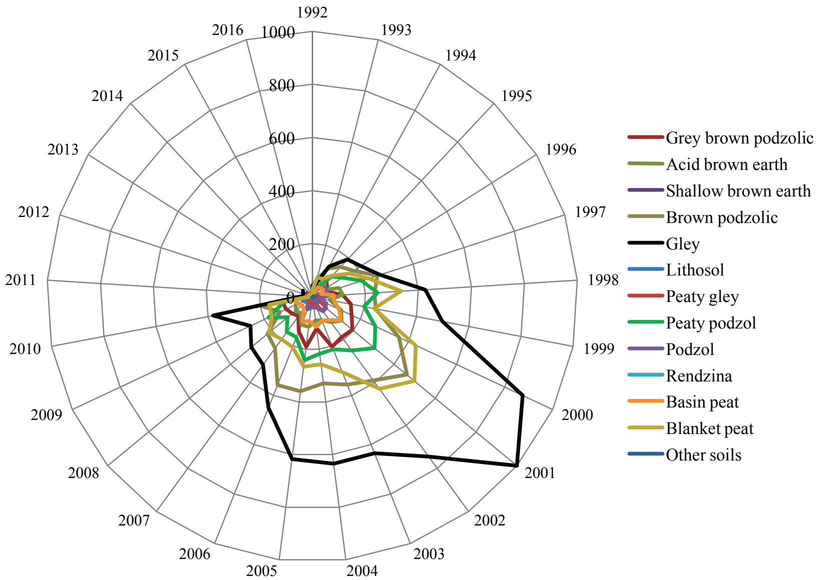

Figure 2: *Annual planting area (ha) for larch species on principle soils from 1970 to present.*

also often higher than that observed in pure stands of those larch species.

Significant correlations were found between the observed yield class of Japanese larch and the yield class of selected companion conifers growing on the same sites (r-values ranging from 0.49 to 0.70; P <0.01) (Figure 3, Table 3). For Japanese larch, the highest correlation was found with the yield class of western hemlock, while for hybrid larch and European larch, the highest correlations were found with Douglas fir (r = 0.73) and Sitka spruce (r = 0.61) respectively. The explanatory power of linear regressions varied for different species combinations (r^2 of 0.24 to 0.48), with the regression analysis for western hemlock (r^2 = 0.48; y = 0.7857x + 11.393) displaying the strongest relationship with the yield class of accompanying Japanese larch (P <0.05). Regression analyses was carried out for Douglas fir, noble fir, Norway spruce and Sitka spruce, stratified by the principle soil groups. These results indicated strong relationships between the yield class of Japanese larch and the yield class of Norway spruce growing together on basin peat (r^2 = 0.71; y = 1.125x + 3) and on gley soils (r^2 = 0.50; y = 0.9364x + 6.6525). The strongest relationship between the yield class of Japanese larch and the yield class of Sitka spruce was found on peaty podzol soils (r^2 = 0.38; y = 0.956x + 8.0091) although it explained a relatively low amount of the variability. A strong relationship was also found between the yield class of Japanese larch and the yield class of Douglas fir on podzolic soils (r^2 = 0.76; y = 1.2632x + 2.6316). These regression equations were developed to help predict growth performance of potential alternative species for larch sites.

A comparison of the performance (yield class) of companion conifers in mixed

Table 2: *Area of larch in mixture with each companion conifer species and productivity of larch in each mixture with productivity of companion species in parenthesis.*

	Area (ha)			Yield class ($m^3ha^{-1}yr^{-1}$)		
Species	**Japanese larch**	**Hybrid larch**	**European larch**	**Japanese larch**	**Hybrid larch**	**European larch**
Corsican pine	32	1	1	7.3 (7.5)	-	-
Douglas fir	495	33	45	10.9 (15.2)	11.5 (16.6)	7.4 (15.6)
European larch	60	11	385	9.9 (7.5)	12.0 (8.0)	7.3[b]
Grand fir	9	1	3	10.0 (16.4)	-	8.0 (17.1)
Hybrid larch	64	504	10	11.3 (10.6)	11.1[b]	8.0 (12.0)
Japanese larch	3,896	62	72	9.7[b]	10.6 (10.8)	7.5 (9.7)
Lawson cypress	30	41	34	10.4 (10.8)	12.0 (10.6)	-
Lodgepole pine (north coastal)	347	27	4	9.0 (10.6)	13.0 (9.6)	8.0 (8.0)
Lodgepole pine (other)	233	18	4	7.2 (6.2)	10.0 (8.0)	5.0 (6.0)
Lodgepole pine (south coastal)	545	45	10	9.0 (11.7)	11.1 (11.9)	6.0 (8.6)
Monterey cypress	5	1	3	-	-	8.0 (20.0)
Monterey pine	11	2	-	8.7 (15.5)	12.0 (14.0)	-
Noble fir	97	3	2	8.4 (13.2)	12.0 (13.0)	6.0 (15.1)
Norway spruce	568	36	133	10.6 (16.6)	12.3 (16.4)	8.1 (15.8)
Other broadleaves[a]	2,110	332	267	-	-	-
Other conifers	45	12	4	-	-	-
Scots pine	394	50	211	9.3 (9.0)	12.0 (9.8)	6.8 (8.9)
Serbian spruce	21	1	-	-	-	-
Silver fir	4	-	1	9.5 (15.4)	-	6.0 (10.0)
Sitka spruce	18,870	1,540	238	10.3 (18.9)	11.1 (18.8)	7.2 (18.5)
Western hemlock	23	23	17	10.4 (16.7)	-	8.7 (14.9)
Western red cedar	-	9	2	10.6 (17.2)	10.7 (14.9)	8.0 (17.5)
Total	**27,859**	**2,752**	**1,446**			

[a] Other broadleaves includes ash, birch, alder, etc.
[b] Indicates a single species stand.

Table 3: *Relationships and strength of relationships between larch and companion species.*

Species	Larch mixture	Soil	Count	Correlation	Standard error	Equation
DF	JL	All	97	0.53	2.85	y = 0.7287x + 7.0311
		Acid brown earth	25	0.68	2.73	y = 1.0471x + 3.5718
		Blanket peat	5	0.49	3.65	y = 2x - 6
		Brown podzolic	37	0.51	3.11	y = 0.7523x + 6.4885
		Gley	4	0.49	4.08	y = 0.6667x + 7
		Peaty podzol	14	0.60	2.11	y = 0.9194x + 5.7097
		Podzol	6	0.87	2.20	y = 1.2632x + 2.6316
GF	JL	All	11	0.55	4.92	y = 1.4167x + 3.1061
NF	JL	All	80	0.49	4.08	y = 0.8659x + 5.4482
		Blanket peat	15	0.56	4.41	y = 1.6731x - 1.1154
		Brown podzolic	17	0.69	3.73	y = 1.0024x + 5.154
		Gley	10	0.36	5.46	y = 0.6389x + 7.9444
		Peaty podzol	20	0.61	3.69	y = 0.9894x + 4.4868
NS	JL	All	92	0.57	2.57	y = 0.6386x + 9.9258
		Acid brown earth	8	0.27	2.49	y = 0.3636x + 11.818
		Basin peat	6	0.84	1.66	y = 1.125x + 3
		Blanket peat	7	0.50	2.42	y = 0.65x + 9.9
		Gley	15	0.71	2.07	y = 0.9364x + 6.6525
		Grey brown podzolic	26	0.46	2.66	y = 0.6014x + 10.322
		Peaty podzol	7	0.34	2.30	y = 0.2941x + 10.235
		Shallow brown earth	12	0.45	2.13	y = 0.3973x + 11.123
SS	JL	All	2,810	0.51	3.51	y = 0.8336x + 10.157
		Acid brown earth	92	0.53	3.22	y = 0.97x + 8.4557
		Basin peat	72	0.48	2.82	y = 0.6002x + 12.392
		Blanket peat	575	0.47	3.54	y = 0.7324x + 10.365
		Brown podzolic	534	0.51	3.28	y = 0.8615x + 10.048
		Gley	690	0.43	3.60	y = 0.1069x + 18.031
		Grey brown podzolic	130	0.32	3.09	y = 0.418x + 15.312
		Lithosol	71	0.55	2.61	y = 0.6672x + 10.36
		Peaty gley	56	0.23	4.88	y = 0.6229x + 13.348
		Peaty podzol	477	0.62	3.18	y = 0.956x + 8.0091
		Podzol	87	0.25	3.61	y = 0.3952x + 14.506
WH	JL	All	10	0.70	2.48	y = 0.7857x + 11.393
WRC	JL	All	7	0.50	5.12	y = 0.9111x + 6.7556
DF	HL	All	7	0.73	0.80	y = 0.8x + 8
NF	HL	All	5	0.31	2.50	y = 0.5x + 7.2
NS	HL	All	5	0.52	3.79	y = 2.25x - 13.5
SS	HL	All	172	0.28	3.08	y = 0.4344x + 14.262
DF	EL	All	21	0.10	3.63	y = 0.1878x + 14.188
NS	EL	All	23	0.45	3.52	y = 1.2302x + 7.0952
SS	EL	All	39	0.61	4.07	y = 1.7474x + 3.7103

[a] Where DF is Douglas fir, EL is European larch, GF is grand fir, HL is hybrid larch, JL is Japanese larch, NF is noble fir, NS is Norway spruce, SS is Sitka spruce, WH is western hemlock and WRC is western red-cedar.

stands with Japanese, hybrid or European larch indicates that Sitka spruce, western red cedar, grand fir, western hemlock, Norway spruce, European silver fir, noble fir and Douglas fir each show higher levels of productivity compared with the larch component across a range of soils (Table 4). Although the pines are currently under threat from *Dothistroma* spp., Monterey pine (*Pinus radiata* D.Don) and lodgepole pine (south and north coastal provenances) showed higher levels of productivity than Japanese and European larches, while Scots and Corsican pines show similar levels of productivity to these larch species, but lower levels of productivity than hybrid larch.

Discussion

This study has highlighted that 32,057 ha of larch species in Ireland are potentially vulnerable to the disease *P. ramorum*. While at first this may appear a relatively small area in terms of total forest extent, the widespread use of larch in mixtures, occupying an area of 165,362 ha (more than 20% of the total area of Irish forests), indicates a more serious issue than at first realised. Although Japanese larch is the primary commercial larch species to be affected by *P. ramorum*, hybrid larch and European larch can also suffer significant damage. In the past, on sites where Japanese larch has become infected, other species (e.g. Sitka spruce, noble fir) in the immediate vicinity have also become infected (but have not succumbed to the disease), which highlights the aggressiveness and adaptability of this pathogen (Brasier and Webber 2010). This is further illustrated by the original "jump" of the pathogen from *Rhododendron* into Japanese larch, which emphasises the uncertainty and unpredictability of the pathogen (Brasier and Webber 2010, O'Hanlon et al. 2016a).

It is possible that larch species have been deployed sub-optimally on poorly-drained soils (gleys, peaty gleys, etc.), often the result of Japanese larch being selected as the secondary species in mixtures with Sitka spruce, widely planted on poorly-drained soils in Ireland. The planting of hybrid and European larch reflects the deliberate policy of matching these species to free draining better-quality soils, whereas Japanese larch was commonly planted to fulfil the mixed species component and provide a contrast of colour in autumn. Much traditional species-site literature recommends the use of European and hybrid larches on moist to free draining soils (e.g. Savill 2013, Pyatt et al. 2001, Wilson 2011), while Japanese larch is believed to have greater tolerance of moist and wet soils (Pyatt et al. 2001). Our results suggest that where larch species are used to form pure stands, more attention is paid to planting the species on optimal soil types, suggesting that better drained and more fertile soils are selected to ensure success. For those minority of mixed larch stands, where Sitka spruce is not a component, it was not anticipated that the larch component would form a valuable part of the final crop, for example European larch in mixture with Norway spruce on frost-prone ground.

This study proposes potential alternative conifer species that offer productive

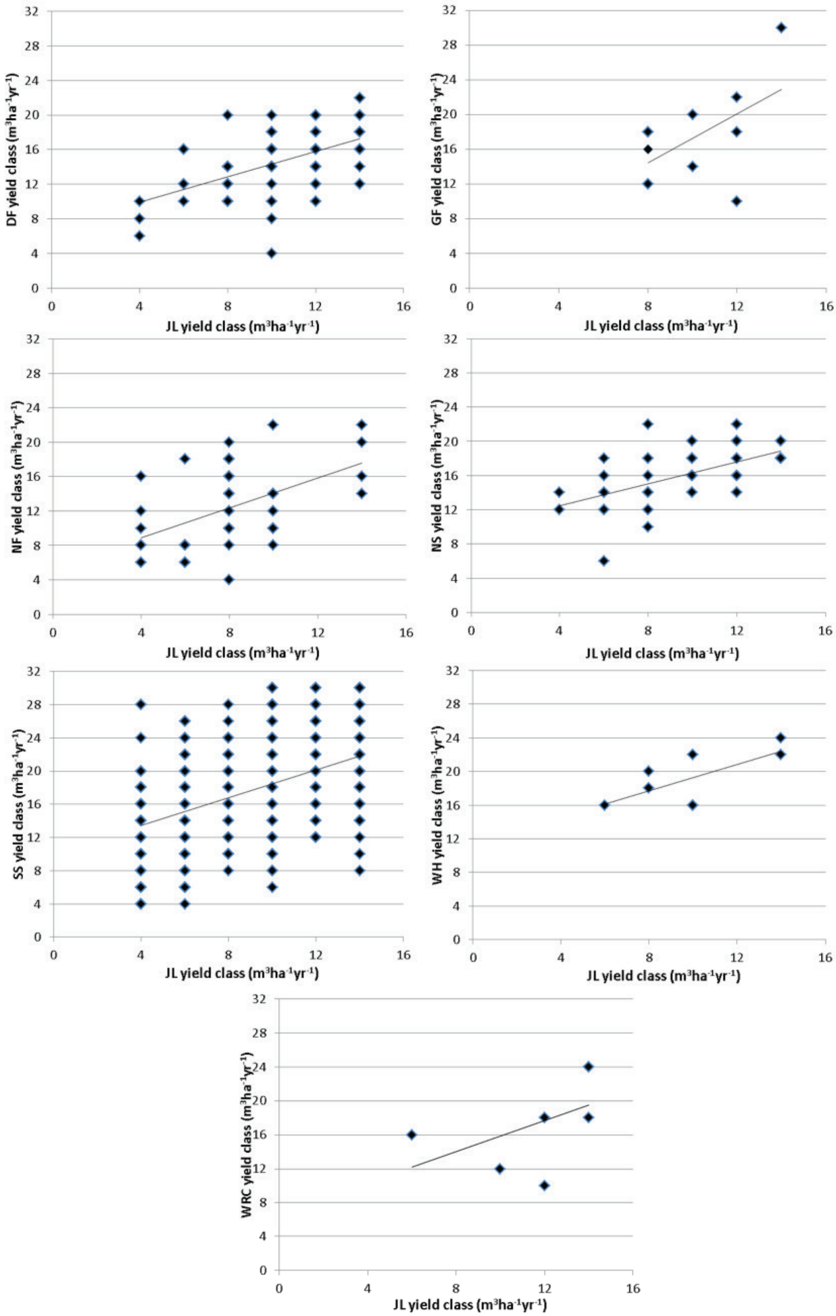

Figure 3: *A comparison of productivity (yield class) of Japanese larch (JL) with that of seven alternative species growing the same site with corresponding correlations in Table 4 (abbreviated species names as defined for Table 3).*

potential on a range of sites where larch is currently grown. Sitka spruce has been used extensively in mixtures with Japanese larch, and results presented here confirm that it remains a suitable species to replace Japanese larch on many sites. This is also the case for hybrid and European larch, where Sitka spruce is the most productive alternative across a range of soil types under current climate conditions. However, any increasing dependence on stands dominated by Sitka spruce comes with potential risks, and the use of alternative conifers in mixtures should be considered to reduce the impact of any potential future biotic attacks on spruce (Cameron 2015). In addition, challenges posed by climate change may necessitate a choice of alternative species better adapted to drier site types (e.g. rendzinas, lithosols, and shallow brown earths). Although Monterey and lodgepole pines can outperform larch species, they are susceptible to *Dothistroma* needle blight. Among the potential alternative conifers, Norway spruce, western red cedar, western hemlock, grand fir, noble fir, European silver fir and Douglas fir show productivity gains over the larch species when grown on suitable sites in each case. Our results and previous literature indicate that Norway spruce and western red cedar might prove useful alternatives on brown earth and brown podzolic soil characterised as being fresh to very moist in soil moisture regime (Pyatt et al. 2001, Wilson 2011, Wilson et al. 2017). Our results also suggest that these may be suitable alternatives for poorly drained gleys and cutaway raised bog soils under Irish conditions, although with uncertainty as to their performance (Horgan et

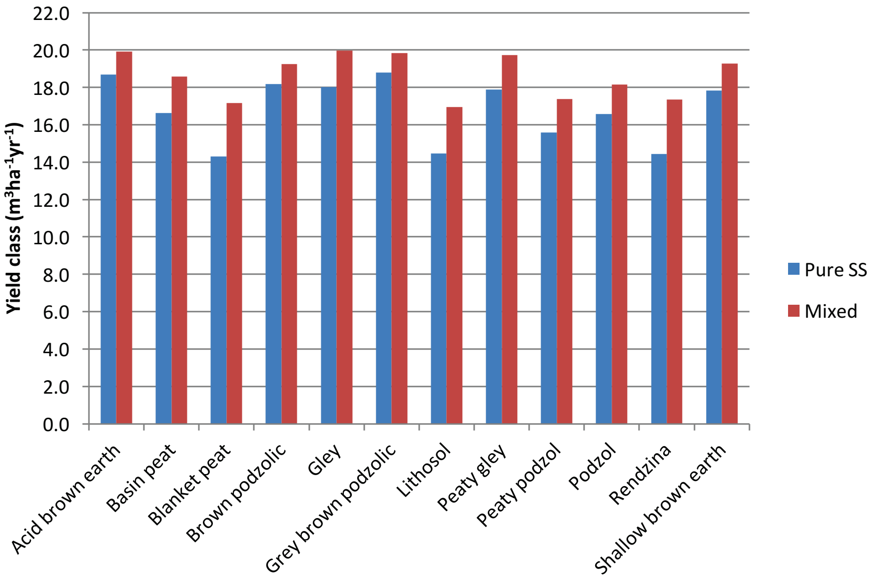

Figure 4: *A comparison of the productivity (yield class) of Sitka spruce (SS) growing in pure and mixed stands with Japanese larch stratified by principle soil type.*

Table 4: *Average productivity of each companion conifer species where found in mixture with larch, stratified by principle soil type.*

Principle soil type	Species[a] (m^3 ha^{-1} yr^{-1})																
	CP	**DF**	**EL[b]**	**GF**	**HL[b]**	**JL[b]**	**LC**	**LP**	**LPNC**	**LPSC**	**MP**	**NF**	**NS**	**SP**	**SS**	**WH**	**WRC**
Acid brown earth	13.5	15.7	7.5	24.0	12.3	11.3	11.5	6.0		11.9	12.0	17.1	17.3	10.2	19.9	18.0	18.0
Basin peat		16.0	7.7	20.0	11.2	10.6	12.0		10.6	13.4	20.0		16.6	9.6	18.6	12.0	18.0
Blanket peat	9.0	13.7	7.2		10.2	9.5	4.0	7.4	10.0	11.3	14.0	12.4	15.7	8.7	17.1	18.0	15.3
Brown podzolic	8.3	15.2	7.3	16.7	11.5	10.5	13.7	12.0	9.3	11.7	15.0	14.4	17.2	9.1	19.1	18.4	16.7
Gley		14.9	7.3	26.0	11.4	10.8	14.0	4.0	10.3	12.2	14.8	13.8	17.9	8.9	20.0	16.0	20.0
Grey brown podzolic	10.0	15.4	7.4	17.3	11.2	10.5	8.0	8.0	11.0	12.3	12.0	13.4	17.5	9.8	19.8		19.3
Lithosol	12.0	15.2	5.6	11.0	9.3	9.8		7.3	9.8	11.7		12.8	19.5	8.4	16.9	12.0	
Peaty gley		13.3	7.0	16.0	11.3	10.6		10.0	12.3	9.4		13.0	15.3	8.0	19.7		
Peaty podzol	6.8	15.0	7.1	15.0	10.7	9.9		4.9	9.4	10.7	16.0	12.8	13.7	8.0	17.3	16.6	14.7
Podzol	8.0	14.4	7.2	18.0	11.4	10.4		8.4	11.1	12.9	12.0	14.3	15.2	9.6	18.5	16.0	
Rendzina			6.8			9.1				12.0			10.0	8.0	17.0		
Shallow brown earth		14.8	7.1	17.0	11.5	9.3	4.0		9.0	14.0		15.0	14.9	6.8	19.1	14.0	

[a] Where CP is Corsican pine, DF is Douglas fir, EL is European larch, GF is grand fir, HL is hybrid larch, JL is Japanese larch, LC is Lawson cypress, LP is lodgepole pine, LPNC is lodgepole pine (north coastal), LPSC is lodgepole pine (south coastal), MP is Monterey pine, NF is noble fir, NS is Norway spruce, SP is Scots pine, SS is Sitka spruce, WH is western hemlock and WRC is western red-cedar.

[b] Indicates a single species stand.

al. 2004). Grand fir, noble fir and European silver fir might prove suitable alternatives on sites classified as having fresh to moist soil moisture regime, including brown earths and imperfectly drained gleys. Although these *Abies* species display reasonable productivity and timber quality (Gil-Moreno et al. 2016), they are vulnerable to drought-crack on moisture limited sites (Savill 2013). Douglas fir and western hemlock might prove useful alternatives for drier sites, both being suited to slightly dry to fresh sites (Anderson 1960, Aldhous and Low 1974). Western hemlock also has the capacity to be extended onto gley soils and some better peats (Burns and Honkala 1990, Wilson 2011, Cameron 2015).

The study indicates that significant positive correlations exist between the productivities of Japanese larch and some companion conifers growing in the same mixed stands. The results of the regression analyses display relationships between the yield class of Japanese larch and companion conifers. For certain potential alternative species on common soil types, it allows the yield class of the alternative species to be predicted satisfactorily from the measured yield class for Japanese larch. We believe that this is a useful tool to assist in predicting the potential of an alternative species on a broader scale while also being assisted by average productivities of companion species across principle soil types (Table 3). Douglas fir, Norway spruce, western hemlock, western red cedar and grand fir (and to a lesser extent noble fir and European silver fir) may offer relevant alternative species with which to increase the resilience of our forests to biotic challenges, provide opportunities for silvicultural diversification and generate more diverse timber products. However, there are specific challenges to wider scale deployment of alternative conifers in Irish forestry. These include unknown risks of potential future biotic agents, increased establishment and maintenance costs (e.g. fencing costs to protect more palatable conifers from deer browsing) and incomplete information on provenance selection, silviculture, marketing and utilisation under Irish forestry conditions.

The selection of alternative conifer species for use in the area currently occupied by Sitka spruce and Japanese larch mixtures is necessary to mitigate future risks of biotic attack. Sitka spruce remains the "species of choice" during afforestation or restocking due to its impressive productivity across a range of soil types and established demand for its timber. In these Sitka spruce/larch plantations, the larch component was primarily used to enhance the landscape visually by providing autumn and winter colour. The autumn colours and deciduous nature of larch facilitated diversity in an otherwise blanket of dark green; it is likely that many conifers mentioned here will not fulfil this objective. Therefore, compatible broadleaved species may be required to improve the visual appearance of forests particularly in upland areas, however it is likely that productivity will be greatly reduced. This study also presented evidence of increased yield associated with Japanese larch mixtures. Japanese larch shows increased yield in mixture over pure stands and a further analysis of Sitka spruce in mixture with Japanese larch performed here indicates an increase in yield associated with mixed stands compared to pure Sitka spruce stands across a range of soils types (Figure 4). While it is known that larch may provide a nursing effect on Sitka spruce (OCarroll 1978), these results suggest that the positive growth effect may persist beyond establishment for both Sitka spruce and Japanese larch. Whether removing the larch in Sitka spruce mixtures may have a detrimental effect on the growth of Sitka spruce remains to be seen. Further research should examine potential nursing effects between other species mixtures.

Many Sitka spruce/Japanese larch mixed stands develop into a Sitka spruce monoculture with the larch component being thinned intensively or completely removed during thinning. Owing to the widespread use of Sitka spruce and Japanese larch mixtures, any replacement species should demonstrate a greater potential for retention to full rotation, be compatible with Sitka spruce (e.g. western hemlock) and offer potential as a nurse species which may assist with the successful establishment and development of the crop. It is likely that the more light-demanding or slower growing conifers may succumb relatively early in the rotation if not released by thinning. Mixtures with slower growing species or species with less dense canopies, such as pines and broadleaved species, may not provide sufficient crown-level competition to control branch and knot size, thus resulting in poor log and timber quality (Cameron 2015). Strategies to allow for the retention of minor species components in mixed stands need further evaluation to include the best methods of deployment including arrangement and composition and to determine whether intimate or non-intimate mixtures may afford greater flexibility in management.

Conclusions

This study suggests a number of alternative species to larch that display higher productivity on suitable sites and still offer lower levels of biotic risk compared to *Larix* spp. or *Pinus* spp. These include Douglas fir, grand fir, Norway spruce, western hemlock and western red cedar, with noble fir and European silver fir also having some potential utility. Depending on the site type, there may be opportunities to choose alternative species that fulfil specific biological or silvicultural functions (e.g. Norway spruce (for late spring or early autumn frost tolerance), Douglas fir (for drought tolerance), and western hemlock (for shade tolerance). Some may also offer enhanced opportunities for applications of alternative silvicultural systems, to improve biotic and abiotic resilience (Mason et al. 2012), assist stand diversification or increase total yield (Mason and Connolly 2014). There may also be a need to consider additional alternative species that are not the direct subject of this study (e.g. Japanese red cedar (*Cryptomeria japonica* (Thunb. ex L.f.) D.Don), coast redwood

(*Sequoia sempervirens* (D.Don) Endl.), Pacific silver fir (*Abies amabilis* (Douglas ex Loudon) Forbes)). Information about their likely performance on a wider range of site types is necessary before wider deployment could be recommended. Further research should focus on the use of mixtures of Sitka spruce with other Pacific coast conifers including Douglas fir, grand fir, western hemlock and western red cedar that may create alternative stand-level models for productive forestry as suggested for Scotland by Cameron and Wilson (2015).

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