This is a repository copy of *Rewilding in the garden : are garden hybrid plants (cultivars) less resilient to the effects of hydrological extremes than their parent species? A case study with Primula*.

Rewilding in the Garden: are garden hybrid plants (cultivars) less resilient to the effects of hydrological extremes than their parent species? A case study with *Primula*

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Abstract

Urban green infrastructure, such as gardens, can mitigate some of the consequences of climate change, e.g. reducing flash-flooding or urban heat islands. Green infrastructure, however, may itself be vulnerable to a changing climate, and not all garden and landscape plant taxa will remain viable under weather scenarios predicted for the future. It has been suggested that cultivated forms of garden plants (hybrids and selected varieties) particularly, will be susceptible to enhanced stress associated with more frequent flooding, drought and rapid oscillations between these hydrological extremes; thus potentially limiting the range of taxa that can be used in gardens in the future. This research explored this concept by evaluating cultivated forms of the common garden plant – *Primula,* and testing whether these were less resilient to the effects of hydrological extremes than their progenitor species, *Primula vulgaris.* The results support this hypothesis and demonstrated that cultivated taxa were more susceptible to the hydrological stresses imposed than *Primula vulgaris.* Interestingly though, those cultivars that superficially resembled the parent species (*Primula* 'Cottage Cream') showed more stress tolerance than others with larger or more ornamental flowers, suggesting a 'gradient of susceptibility' within the hybrids. The notion that the most flamboyant cultivars are sacrificing stress tolerance for traits linked with aesthetics is discussed. The data, albeit on one genus only, has implications for the design of gardens/ornamental landscapes for the future and calls for more attention within breeding programmes to enhance abiotic stress tolerance within garden and landscape plants.

Keywords Climate change · Drought · Green infrastructure · Landscape · Ornamental · Waterlogging

Introduction

Urban green space is considered an asset in partially mitigating the effects of climate change on towns and cities. Ecosystem services associated with urban green space include, aerial and surface cooling (Oliveira et al. 2011; Blanusa et al. 2013), reduced risk of flooding through the capture/storage of rainwater (Oberndorfer et al. 2007), improved air quality (Baro et al. 2014) and providing habitat for wildlife, much of which is under pressure from a changing climate (Rudd et al. 2002; Rupprecht et al. 2015). Indeed, many policy makers now recognise that urban green space has a key role in 'future proofing' cities against climate change (Demuzere et al. 2014). Yet urban green space itself will not be immune to the effects of a changing climate.

The impact of climate change has been well-documented for natural landscapes and ecosystems (Pecl et al. 2017), as well as for global agriculture (Wiebe et al. 2015). There are significant risks for urban vegetation too, with threats from drought, flooding and new biotic factors (Tubby and Webber 2010; Savi et al. 2015; Webster et al. 2017). Such risks have stimulated discussion on appropriate plant selection to increase the resilience of urban green space in future. These discussions have tended to focus on the choice of street and park trees, where careful genotype selection is required to ensure trees have genuine longevity within a climate that is changing and unpredictable (Roloff, 2009; Sjöman et al. 2015).

One area that has received little attention though, is garden landscapes. Yet private gardens comprise 15–25% of total

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urban area (Gaston et al. 2005; Mathieu et al. 2007), and along with significant areas of public gardens, heritage gardens, allotments and municipal amenity landscapes (planted roadways, roundabouts, containers, raised beds etc.) provide a significant proportion of the total ecosystem service delivery within a city (Cameron et al. 2012; Cameron and Hitchmough 2016). Gardens have a high proportion of non-native plant species and represent landscapes where the composition and density of plant species are artificially regulated through design and management (Niemelä 1999; Thompson et al. 2003). Moreover, the majority of taxa intentionally planted are either selected forms (varieties) or hybrids between different species leading to a plethora of cultivated forms (cultivars). Within the genus *Rhododendron*, for example, there are thought to be over 28,000 different cultivars (Leslie 2004).

Most cultivated ornamental plants in a garden have been selected/bred for their aesthetic qualities (attractive flowers, foliage, bark or fruit), with perhaps less attention paid to their tolerance of abiotic and biotic stress factors. This is partially due to the fact that gardens and other designed landscapes are actively-managed to reduce biological competition (e.g. hoeing to eliminate weeds and pesticides or biocontrol agents used to control invertebrate pests or fungal/bacterial pathogens) as well as to mitigate abiotic factors such as providing addition nutrients (fertilizer application) or avoiding drought stress through artificial irrigation (Milla et al. 2015). Consequently, the selection protocols for garden plants have emphasised form and aesthetics over intrinsic resistance and resilience to stress (Cameron and Blanuša 2016). Formally, resistance is the ability for a plant to tolerate stress whereas resilience relates to an ability to recover from a given stress, however, for simplicity in this text we use the term 'resilience' to denote a plant's ability to survive one or more stress events. Enhancing resilience to abiotic stress is rarely the top priority in ornamental breeding programmes, and when it is considered tends to focus on expanding thermal tolerances within a genus (Susko et al. 2016; Kuligowska et al. 2016). There is an assumption that highly-cultivated ornamental varieties, particularly those that invest heavily in floral displays, are less tolerant of abiotic stress than less flamboyant varieties or their wild predecessors. Interestingly, there is limited evidence of this being tested empirically or through any systematic procedures. Rather the idea is based on anecdotes from gardeners, supported by 'trade-offs' that are known to occur in other breeding programmes, such as for agronomic crops (Denison 2012).

Currently, intensive management is allowing highly-bred, flamboyant ornamentals to perform well in garden settings. If climate change continues to track predictions, however, the ability to buffer plants against environmental stress through careful management may be diminished. This raises the question, will cultivated forms of garden plants remain viable as climate change induces more extreme and variable weather patterns? Indeed, does the current process of selecting/breeding new plants for novel or greater aesthetic traits undermine the resilience of garden plants to a changing climate? If so, this could have significant consequences for the garden flora of the future, with much reduced diversity and a greater reliance on a relatively limited range of robust, true species. This itself has implications for the potential range and extent of ecosystem services that garden and other ornamental designed landscapes can provide (Cameron and Blanuša 2016).

This paper uses the UK climate impact models (Jenkins and Perry 2008) to create hydrological scenarios that garden plants may face in the future. In the UK, predicted increases in climatic variability, particularly with respect to precipitation patterns (IPCC, 2013; Simpson and Jones 2014), are expected to present a challenge for the sustainable management of designed landscapes. Climate models forecast a shift towards less frequent but heavier rainfall (Hegerl et al. 2011), a trend largely consistent with recent increases in rainfall intensity (Osborn et al. 2000). This redistribution of rainfall has been linked to increases in both the severity of droughts and the frequency of flooding (Fay et al. 2003; Trenberth et al. 2003). Infrequent high-intensity rainfall is less able to infiltrate soils, and instead causes runoff and localised flooding rather than replenishing moisture within the soil profile (Trenberth 2005). Although, these trends are increasingly recognised, particularly within the ecological literature (Knapp et al. 2008; Reyer et al. 2013; Walter et al. 2013), findings are not directly transferable to garden systems as the external forces that govern plant population and community dynamics are profoundly different (Purugganan and Fuller 2009). Hence, this research aims to develop realistic hydrological scenarios and determine how landscape plants under cultivation vary in their responses to these.

In the UK, as elsewhere, increases in the frequency of previously 'extreme' climatic events, may result in traditional planting styles and garden practices becoming unsustainable (Webster et al. 2017). As planting design plays a fundamental role in determining ecosystem function (Hunter 2011), the careful selection of 'robust' ornamentals may offer a means to establish greater climatic resilience in both public and private gardens. However, a lack of quantifiable data on ornamental plant tolerances, particularly with respect to extreme events, represents a significant barrier in moving towards this goal. This research, therefore exploits *Primula* as a model genus to determine how degree of cultivation affects a genotype's capacity to tolerate hydrological stresses associated with a changing climate. We hypothesise that *Primula vulgaris*, a widely distributed UK native species, will show greater resilience to hydrological stress treatments than cultivated 'garden' forms of *Primula*. Moreover, the performance of cultivars will decrease with greater visual deviation from this wild species. In one experiment, we also introduce two

other UK native *Primula* species as comparators, *P. excelsior* and *P. veris,* again with the hypothesis that they will outperform the cultivated varieties of *P. vulgaris* in general stress tolerance, despite being associated with relatively narrow eco-physiological profiles, i.e. preference for wetter and drier regimes, respectively.

Material and methods

Primula as a model genus

Primula species and cultivars are popular garden plants, being represented within mainstream bedding-plant taxa (i.e. those planted out in flower 'beds' *en masse* to provide extensive displays of colour), as well as commonly used as herbaceous perennials in borders and woodlands, with certain species also being well-adapted respectively, to bog gardens (e.g. *Primula bulleyana*) or to more drought-prone 'alpine' rockeries (e.g. *Primula allionii*). *Primula vulgaris* was selected for this research given that both the wild species and cultivated varieties are widely used as ornamentals across temperate parts of the globe (Hayta et al. 2016). The wild *P. vulgaris* is a spring flowering perennial (naturally distributed across Europe, south-west Asia and northern Africa), and is associated with a range of habitats, from woodlands and hedgerows to unsheltered grasslands and heaths (Jacquemyn et al. 2009). It has been extensive bred to provide new cultivars that improve the uniformity and seasonality of flowering, in addition to enhancing the flower size and colour (Karlsson 2001). Consequently, the majority of cultivars now in existence are similar in overall size to the wild species but generally offer more substantial floral displays in an extensive range of colours. As with many commercial ornamental plants, the ancestry of these cultivars is not well documented. Therefore, the degree of cultivation is discussed relative to the morphological divergence from the wild species (i.e. variations due to flower size and colour).

Plant material

Primula vulgaris (pale yellow flowers, 20–30 mm dia.) was selected as the main model species and included in all experiments. Cultivated forms of *P. vulgaris* were compared for their resilience to wet and dry regimes. These included i. *Primula* F1 'Cottage Cream' (*P.* 'Cottage Cream') which resembles the wild species but is marginally more compact and has a reputation for reliable, consistent flowering, with flowers 22–35 mm dia.; ii. Plants from the *Primula* F1 'Alaska' strain, namely 'Alaska – White with Orange Eye' (*P.* 'Alaska WOE'), *P.* 'Alaska-Blue', *P.* 'Alaska-Orange' and *P.* 'Alaska-Rose'; all the Alaska strain cultivars have large flowers 35–50 mm dia.; iii. *Primula* 'Forza' – with pink/

peach flowers 22–35 mm dia. In addition, two other native species of *Primula,* i.e. *P. veris* and *P. elatior* were included in one experiment. *Primula veris* has an intermediate UK distribution but is only associated with well-drained natural habitats and is notably absent from much of the west of the UK (with higher rainfall patterns) (Brys and Jacquemyn 2009). Finally, *P. elatior* has a much more restricted UK distribution, being naturally confined to wet sites typically in woodlands and meadows (Taylor and Woodell 2008). Despite the natural distribution patterns, both these species are also used relatively commonly as garden plants. For all taxa, seed-raised plug plants were purchased and transplanted into 90 mm pots using a 3:1 mix of Levington M3 compost (95% fine peat, 5% coir with 233 g N, 104 g P and 339 g K m^{-3}, pH: 5.3–6.0: Scotts, Frimley, Surrey, UK) and perlite, and grown-on in a glasshouse (18-22 °C) at the University of Sheffield, UK. Batches of plants were potted on 28 Nov. 2014 (Exp. 1) 15 Jan. 2015 (Exp. 3) and 28 Sep. 2015 (Exp. 2) prior to experimentation (see below).

Three separate experiments were implemented to determine the effects of wetting and drying combinations/cycles on *Primula* taxa. The research adopted a range of experimental approaches, utilising semi-controlled conditions within a glasshouse (Exp. 1), semi-natural conditions (polythene 'rain-shelters' outdoors, Exp. 2) as well as a garden condition representing a more realistic, albeit less controllable, scenario (Exp. 3).

Experiment 1. The influence of waterlogging and drought stress in *Primula* taxa, and the effect of repeated or alternated stress

The aim of this experiment was to determine how cultivated taxa of *Primula* performed compared to their parent species (*Primula vulgaris*), when exposed to combinations of drought and waterlogging. Plants of four taxa (*P. vulgaris*, *P.* 'Cottage Cream', *P.* 'Alaska WOE' and *P.* 'Forza'- Fig. 1) were re-potted into 130 mm pots on 28 Feb. 2015 and grown-on under glass (with a day/night regime of 12 h 24 °C/12 h 18 °C and

Fig. 1 Flowers of the four taxa used in Exp. 1. From left to right – *Primula vulgaris*, *P.* 'Cottage Cream', *P.* 'Forza' and *P.* 'Alaska WOE'

supplementary lighting [Helle Lamps, IR 400 HPS, 400 W] to ensure a consistent photoperiod and photosynthetic photon flux density > 1000 µmol m^{-2} s^{-1}). Irrigation treatments were initiated on 13 Apr. 2015 and included a double stress treatment where plants were exposed to either drought or waterlogging, followed by a recovery phase (3 wk) before a second stress period composed of the same stress again or the alternative stress factor. Thus treatments were; double drought (DD), drought/waterlogging (DW), waterlogging/drought (WD), double waterlogging (WW) or an un-stressed control group (CC) (Table 1). Additional plants were harvested after the initial stress period to determine impact on biomass at this stage.

Control plants were watered weekly. In contrast, drought treatments comprised withholding irrigation for 3 wks, whereas waterlogging constituted placing a plant in a water bath, so the growing media was flooded to the surface, and kept saturated for 1 wk. Preliminary studies (data not shown) demonstrated that physiological effects of drought occurred 12–14 d after irrigation ceased, whereas equivalent responses occurred after only 2–3 d of waterlogging, as such the period water was withheld (3 wks), was not equal to the period of waterlogging (1 wk) (Table 1). Each treatment was represented by 8 replicate plants per taxa, randomly distributed across the glasshouse bench. Plants were recorded for quality every 3–4 d and destructive harvests implemented on 30 Jul. 2015. Data is presented for key phases only – before stress, after 1st stress, during recovery phase 1, after 2nd stress and during recovery phase 2, relating to 0, 22 40, 64 and 77 d of the experiment respectively.

Experiment 2. Performance of *Primula* taxa when exposed to alternative rainfall scenarios during winter and spring

Treatments were implemented to consider the impacts of seasonally redistributed rainfall on plant performance. As such, plants experienced either a 'control' or alternatively a 'wet' winter (Dec. 2015- Mar. 2016), followed by a 'control', 'wet' or 'dry' spring/summer (Apr. 2016-Aug. 2016). Control treatments were based on the seasonal average rainfall calculated from the 1981–2010 Sheffield Central data set. Wet treatments then received a 40% increase whilst dry treatments received a 40% reduction relative to the seasonal mean calculated from the historical data (Table 2).

The study was conducted outdoors at the University of Sheffield, South Yorkshire, UK. A single plant from each taxon (*P. vulgaris*, *P. elatior*, *P. veris*, *P.* 'Cottage Cream', *P.* 'Alaska WOE' and *P.* 'Forza') was randomly located within small experimental plots (trays 600 × 400 × 200 mm). Forty-eight experimental plots were used and distributed between the 6 irrigation treatments placed within 3 open-ended 'rain-shelter' polytunnels. Polytunnels were covered in translucent PVC to excluded natural rainfall but facilitate a PPFD of between 460 and 1450 µmol m^{-2} s^{-1}. Controlled volumes of water were then supplied evenly across the plots using 6 drippers per plot. Plants were monitored weekly with final quality assessments terminated 16 Aug. 2016.

Experiment 3. Garden performance of *Primula*, comparing the species *P. vulgaris* and 3 taxa within the *Primula* Alaska strain

A final experiment determined how cultivated *Primula* taxa performed in an *in vivo* garden situation, when exposed to naturally varying hydrological regimes. Three hybrids of *Primula* from the Alaska strain (*P.* 'Alaska Blue', *P.* 'Alaska Orange' and *P.* 'Alaska Rose') were compared with *P. vulgaris*; ideally specimens of *P.* 'Alaska WOE' would also have been included, but these were undersized at time of planting. A garden in Skelton, East Yorkshire, UK. (53°42′ 46.10″N; 0°50′12.16″W) was chosen due to its heavy clay-loam floodplain soil, where a naturally-high ground water table could cause surface flooding on occasions, but also

Table 1 Exp. 1. Watering regimes implemented to treatments over the course of the experiment. Treatment codes correspond to CC = control, DD = double drought, WW = double waterlogging, DW = drought & waterlogging and WD = waterlogging & drought, respectively

Days												
	1	7	14	21	28	35	42	49	56	63	70	77
CC	+	+	+	+	+	+	+	+	+	+	+	+
DD	−	−	−	+	+	+	−	−	−	+	+	+
DW	−	−	−	+	+	+	+	+	+++	\	\	+
WD	+	+	+++	\	\	+	−	−	−	+	+	+
WW	+	+	+++	\	\	+	+	+	+++	\	\	+

(+) indicates pots were watered to container capacity, (−) indicates water was withheld, (+++) indicates pots were flooded to the surface of the growing media and (\) indicates wet media was allowed to dry naturally

Table 2 Exp. 2. Irrigation treatments as applied over the course of the experimental period Treatment codes correspond to C = control, D = dry and W = wet

Treatment	Winter Irrigation	Spring/Summer Irrigation
C/D	Control (77 ml per month)	−40% (36 ml per month)
C/C	Control (77 ml per month)	Control (61 ml per month)
C/W	Control (77 ml per month)	+40% (85 ml per month)
W/D	+40% (107 ml per month)	−40% (36 ml per month)
W/C	+40% (107 ml per month)	Control (61 ml per month)
W/W	+40% (107 ml per month)	+40% (85 ml per month)

Winter treatments were applied from the start December to end March. Spring/Summer treatments were applied between the start April to the end of August

where the soil could desiccate, shrink and crack after prolonged dry periods. To escalate the potential stress plants may experience, control plots at ground level (2.5 × 2.5 m, l x b) were augmented with raised plots (300 mm above) and sunken plots (300 mm below) ground level. It was anticipated that the raised plots would improve drainage in the winter, but enhance risk of moisture deficits in summer, and conversely, sunken plots may predispose plants to winter waterlogging, but have greater moisture availability in summer. All plots comprised the parent clay soil without supplementary fertilizer, cultivated to a 'crumb structure' before planting. Each plot treatment (height) was represented by 2 plots each, and each taxon represented by 5 replicate plants per plot. Plants were planted 450 mm apart in a randomised manner on 24 Feb. 2015 and watered until established - 30 May 2015. Soil moisture status was monitored weekly (ML3 ThetaProbe Soil Moisture Sensor and HH2 Moisture Meter, Delta-T, Devices, Cambridge, UK) with data meaned from three samples per plot. The presence of any standing surface water was also noted. Plants were monitored for survival, growth and flower numbers present on a monthly basis and the experiment terminated on 24 Jun. 2016.

Data collection across experiments

Plants were monitored for survival (%) and visual quality. Plants were assessed visually following Zollinger et al. (2006), where they were scored separately on degree of wilting, chlorosis and senescence based on a ranking 0–5 in each case. Scores across the three scales were combined to give each plant a total score out of 15. Flowers were also recorded for number per plant (flower score) or as biomass.

Chlorophyll florescence was used to determine levels of stress imposed in the first two experiments. The maximum quantum efficiency of PSII photochemistry (F_v/fm) was measured twice weekly (Handy PEA -Plant Efficiency Analyser, Hansatech Instruments, Kings Lynn, UK) on three randomly selected dark-adapted (30 min.) leaves per plant. The three measurements were meaned to obtain a single F_v/fm for each plant. Lower values occur when a plant is exposed to stress and indicate inactivation of PSII (photoinhibition) (Björkman and Demmig 1987; Murchie and Lawson 2013).

At the end of experimental periods (Exp. 1 and 2), plants were harvested and assessed for final biomass. Roots were washed and separated from above-ground material (topgrowth). Dead leaves and stems were removed and biomass was dried (80 °C for 72 h), before dry weights were recorded. In some experiments top-growth was also assessed nondestructively by estimating the area of ground the plant covered. The longest leaf was identified and length from the centre of the plant measured (radius 1). A leaf at 90° around from this was also measured (radius 2) and a mean radius value calculated. The surface area was then estimated from $A = \pi r^2$.

Statistical analysis

Analysis of visual assessments for quality, chlorophyll florescence, flower scores and plant coverage were analysed using ANOVA, with significant levels between means compared via Tukey post-hoc tests. Where variance in data was insufficient or the design unbalanced ANOVA was not applied (NA) and mean values only are presented. Percentage survival was calculated using visual quality scores, where 0 was taken to mean plant death. The dry weight of roots and shoots, and change in biomass between the treatments were analysed using the Welsh Test as assumptions of homogeneity of variance were violated, with subsequent treatment differences identified by Games-Howell tests. Analyses were conducted through 'R' version 3.3.1. For large data sets, data and analysis was restricted to a single taxon for ease of presentation (e.g. Exp. 1) otherwise comparisons across taxa were included where appropriate (e.g. Exp. 3). Data are depicted in tables/figures as mean values, with significant differences between treatments denoted by letters.

Results

Experiment 1. The influence of waterlogging and drought stress in *Primula* taxa, and the effect of repeated or alternated stress

In *P. vulgaris*, exposure to drought during the first stress phase significantly reduced visual plant quality (DD and DW) and Fv/fm values (DW only), but scores improved again during the first recovery phase (Table 3). During the second stress, exposure to waterlogging or drought reduced visual scores compared to controls, but there was no effect on Fv/fm. On recovery, plants generally improved in visual quality, except for those previously exposed to WW (10.9) where quality remained significantly lower than controls (13.7, Table 3). Notably, all plants of *P. vulgaris* survived, irrespective of the stress combinations imposed (Table 3).

Drought also had a significant effect in *P.* 'Cottage Cream' during the first stress phase, but visual values did not always recover to that of controls during the first recovery phase, (i.e. 11.9 for DD, Table 4). A second drought episode reduced visual quality further (7.6 for DD) and caused some plant fatalities in DD (Table 4). Visual quality scores for DD, however, were not significantly different to those of the controls at the second recovery phase. In contrast, quality was significantly reduced in plants first waterlogged then exposed to drought (WD) when compared to controls (i.e. 10.0 vs 13.3, Table 4). Stress events reduced Fv/fm values, but these were rarely significantly different. Overall survival rate was high in *P.* 'Cottage Cream' with fatalities only associated with DD.

Table 3 Exp. 1. *P. vulgaris*: Visual scores, chlorophyll fluorescence values and survival percentages at different phases of the experiment, $n = 8$. Treatment codes correspond to CC = control, DD = double drought, WW = double waterlogging, DW = drought & waterlogging and WD = waterlogging & drought, respectively. *NB Up to recovery phase 1 only the first letter of the treatment designation is relevant,* e.g. *DD plants have only been exposed to one period of drought.* Sig. = significance level; NA = Anova not applied; NS = not significant. Superscript letters denote significant differences between treatments at that phase

	Treatment					
	CC	DD	WW	DW	WD	Sig.
Visual						
Before stress	15.0	14.9	15.0	14.9	14.9	NA
After 1st stress	14.4 [a]	9.0 [b]	14.0 [a]	8.3 [b]	13.4 [a]	$P < 0.001$
Recovery phase 1	14.0 [a]	12.7 [a]	13.3 [a]	13.0 [a]	13.3 [a]	NS
After 2nd stress	13.9 [a]	11.2 [b]	10.7 [b]	11.8 [b]	11.3 [b]	$P = 0.002$
Recovery phase 2	13.7 [a]	12.3 [ab]	10.9 [b]	12.4 [ab]	11.8 [ab]	$P = 0.017$
Ch. Fl. (Fv/fm)						
Before stress	0.82 [a]	0.82 [a]	0.82 [a]	0.83 [a]	0.83 [a]	NS
After 1st stress	0.81 [a]	0.71 [ab]	0.81 [a]	0.62 [b]	0.80 [a]	$P = 0.003$
Recovery phase 1	0.82 [a]	0.79 [a]	0.77 [a]	0.79 [a]	0.80 [a]	NS
After 2nd stress	0.79 [a]	0.72 [a]	0.73 [a]	0.78 [a]	0.77 [a]	NS
Recovery phase 2	0.75 [a]	0.75 [a]	0.64 [a]	0.73 [a]	0.74 [a]	NS
Survival (%)						
Recovery phase 1	100	100	100	100	100	NA
Recovery phase 2	100	100	100	100	100	NA

Exposure to the first stress reduced plant quality in *P.* 'Alaska WOE', irrespective of whether it was waterlogging or drought (Table 5). Most plants recovered, the exception being some of the specimens exposed to waterlogging (e.g. 9.7 for WW). A second period of stress generally reduced quality again, but only significantly so for the WW treatment

Table 4 Exp. 1. *P.* 'Cottage Cream': Visual scores, chlorophyll fluorescence values and survival percentages at different phases of the experiment, n = 8. Treatment codes correspond to CC = control, DD = double drought, WW = double waterlogging, DW = drought & waterlogging and WD = waterlogging & drought, respectively. *NB Up to recovery phase 1 only the first letter of the treatment designation is relevant,* e.g. *DD plants have only been exposed to one period of drought.* Sig. = significance level; NA = Anova not applied; NS = not significant. Superscript letters denote significant differences between treatments at that phase

	Treatment					
	CC	DD	WW	DW	WD	Sig.
Visual						
Before stress	14.7	14.3	14.7	14.0	14.1	NA
After 1st stress	14.4 [a]	8.43 [b]	13.6 [a]	11.3 [ab]	13.3 [a]	$P < 0.001$
Recovery phase 1	13.9 [a]	11.9 [b]	12.7 [ab]	13.0 [ab]	13.0 [ab]	$P = 0.019$
After 2nd stress	13.1 [a]	7.6 [b]	10.6 [ab]	10.7 [ab]	9.9 [ab]	$P = 0.013$
Recovery phase 2	13.3 [a]	11.4 [ab]	11.3 [ab]	11.6 [ab]	10.0 [b]	$P = 0.049$
Ch. Fl. (Fv/fm)						
Before stress	0.83	0.83	0.82	0.80	0.82	NA
After 1st stress	0.80 [a]	0.63 [a]	0.78 [a]	0.74 [a]	0.80 [a]	$P = 0.050$
Recovery phase 1	0.79 [ab]	0.70 [b]	0.81 [a]	0.78 [ab]	0.80 [ab]	$P = 0.023$
After 2nd stress	0.77 [a]	0.55 [a]	0.72 [a]	0.75 [a]	0.60 [a]	NS
Recovery phase 2	0.78 [a]	0.63 [a]	0.71 [a]	0.74 [a]	0.60 [a]	NS
Survival (%)						
Recovery phase 1	100	100	100	100	100	NA
Recovery phase 2	100	86	100	100	100	NA

Table 5 Exp. 1. *P.* 'Alaska WOE': Visual scores, chlorophyll fluorescence values and survival percentages at different phases of the experiment, n = 8. Treatment codes correspond to CC = control, DD = double drought, WW = double waterlogging, DW = drought & waterlogging and WD = waterlogging & drought, respectively. *NB Up* to recovery phase 1 only the first letter of the treatment designation is relevant, e.g. *DD* plants have only been exposed to one period of drought. Sig. = significance level; NA = Anova not applied; NS = not significant. Superscript letters denote significant differences between treatments at that phase

	Treatment					
	CC	DD	WW	DW	WD	Sig.
Visual						
Before stress	14.1 [a]	13.3 [a]	14.3 [a]	14.0 [a]	14.0 [a]	NS
After 1st stress	14.6 [a]	8.3 [b]	11.0 [b]	10.9 [b]	11.0 [b]	$P < 0.001$
Recovery phase 1	14.3 [a]	12.6 [ab]	9.7 [b]	12.9 [ab]	12.4 [ab]	$P = 0.024$
After 2nd stress	13.9 [a]	9.4 [ab]	8.0 [b]	11.9 [ab]	11.7 [ab]	$P = 0.020$
Recovery phase 2	14.0 [a]	11.0 [ab]	8.1 [b]	11.9 [ab]	12.0 [ab]	$P = 0.050$
Ch. Fl. (FV/fm)						
Before stress	0.82	0.81	0.83	0.82	0.82	NA
After 1st stress	0.81 [a]	0.73 [a]	0.72 [a]	0.77 [a]	0.80 [a]	NS
Recovery phase 1	0.81 [a]	0.76 [a]	0.65 [a]	0.81 [a]	0.80 [a]	NS
After 2nd stress	0.79 [a]	0.68 [a]	0.48 [b]	0.79 [a]	0.78 [a]	$P = 0.048$
Recovery phase 2	0.78 [a]	0.68 [a]	0.54 [a]	0.77 [a]	0.77 [a]	NS
Survival (%)						
Recovery phase 1	100	100	100	100	100	NA
Recovery phase 2	100	86	71	100	100	NA

(8.0), with visual values remaining low even during the second recovery period (Table 5). The WW treatment was associated with reductions in Fv/fm, and although some plants recovered, approximately 30% of *P.* 'Alaska WOE' specimens eventually died. Some fatalities (14%) were also noted in DD.

Primula 'Forza' was susceptible to loss of quality (and viability) to both drought and waterlogging. Unlike other taxa, both visual and Fv/fm values tended to continue to decrease during the first recovery phase (Table 6), corresponding to a number of fatalities at this stage. Exposure to a second round of stress reduced quality across all treatments, with lowest scores and highest fatalities associated with the DD and WD treatments, where only 14% of plants survived (Table 6).

After the initial stress event, there was no significant effect on biomass in any taxa (data not shown). After the second stress period, there was no effect on shoot biomass in *P. vulgaris* or *P.* 'Cottage Cream' but in the former, root biomass was reduced in DW compared to WD (Table 7). In *P.* 'Alaska WOE', shoot and root biomass was reduced in all treatments compared to controls except WD (shoots only). In *P.* 'Forza', both shoot and root biomass loss was greatest in treatments associated with the initial waterlogging (WD and WW). Flowers contributed a relatively small proportion of biomass, with the exception of *P.* 'Forza', which was relatively floriferous (Table 7).

Of the four taxa evaluated, *P. vulgaris* showed the most resilience, closely followed by *P.* 'Cottage Cream'. *Primula* 'Alaska WOE' showed some intermediate levels of tolerance, although it was most susceptible to a double waterlogging treatment. In contrast, *P.* 'Forza' showed limited tolerance to waterlogging or drought and overall was the least resilient taxon.

Experiment 2. Performance of *Primula* taxa when exposed to alternative rainfall scenarios during winter and spring

Primula 'Forza' was the most damaged cultivar, showing some fatalities and loss of quality after a wet winter (W/C) (Fig. 2), but also intolerance to either a dry or wet spring-summer, especially after a previous wet winter i.e. (W/D and W/W) (Fig. 2). Treatments had no effect on *P. vulgaris*, and by the end of the experiment all plants demonstrating similar quality scores (Fig. 3) and 100% survival. *Primula veris* on the other hand, lost quality in the wet winter/wet spring-summer scenario (W/W), with 50% fatalities; whereas *P. elatior* had marginal non-significant quality reductions associated with control winter/dry spring-summer (C/D).

Above ground biomass tended to be greatest with *P. vulgaris*, but there were no significant differences due to treatment in any of the taxa (data not shown). Of the plants that survived though, specimens tended to have smaller canopies in *P. veris* W/D; *P.* 'Cottage Cream' W/W; *P.* 'Alaska WOE' C/D, C/W, W/D, W/W and *P.* 'Forza' W/W (Table 8).

Table 6 Exp. 1. *P.* 'Forza': Visual scores, chlorophyll fluorescence values and survival percentages at different phases of the experiment, n = 8. Treatment codes correspond to CC = control, DD = double drought, WW = double waterlogging, DW = drought & waterlogging and WD = waterlogging & drought, respectively. *NB Up to recovery phase 1 only the first letter of the treatment designation is relevant, e.g. DD plants have only been exposed to one period of drought.* Sig. = significance level; NA = Anova not applied; NS = not significant. Superscript letters denote significant differences between treatments at that phase

	Treatment					
	CC	DD	WW	DW	WD	Sig.
Visual						
Before stress	14.9 [a]	14.6 [a]	14.6 [a]	14.6 [a]	14.1 [a]	NS
After 1st stress	14.0 [a]	7.4 [b]	10.7 [ab]	11.9 [ab]	7.0 [b]	$P = 0.050$
Recovery phase 1	14.1 [a]	6.3 [bc]	9.1 [abc]	10.1 [ab]	1.7 [c]	$P < 0.001$
After 2nd stress	13.9 [a]	1.6 [c]	5.3 [bc]	8.6 [ab]	1.6 [c]	$P < 0.001$
Recovery phase 2	14.1 [a]	1.6 [b]	3.7 [b]	4.6 [b]	2.1 [b]	$P < 0.001$
Ch. Fl. (FV/fm)						
Before stress	0.81	0.80	0.81	0.81	0.80	NA
After 1st stress	0.80 [a]	0.55 [b]	0.75 [ab]	0.76 [ab]	0.69 [ab]	$P = 0.020$
Recovery phase 1	0.80 [a]	0.35 [ab]	0.61 [a]	0.68 [a]	0.13 [b]	$P = 0.001$
After 2nd stress	0.80 [a]	0.11 [c]	0.34 [bc]	0.59 [ab]	0.04 [c]	$P < 0.001$
Recovery phase 2	0.80 [a]	0.09 [b]	0.20 [b]	0.30 [b]	0.11 [b]	$P < 0.001$
Survival (%)						
Recovery phase 1	100	57	86	86	57	NA
Recovery phase 2	100	14	43	57	14	NA

Experiment 3. Garden performance of *Primula*, comparing the species *P. vulgaris* and three taxa within the Primula Alaska strain

Moisture levels in garden soils ranged between 0.35–0.46 m³ m⁻³ during winter, but no significant differences overall were noted between treatments (i.e. based on plot level). Values were less in summer, decreasing to 0.27 m³ m⁻³ during Aug. 2015 in one raised plot, but there was no evidence of plant injury at this point. Surface water (puddling) was noted in the ground level and sunken plots on 12–14 Dec. 2015 and 7 Feb. 2016, with additional surface water also apparent for the sunken plots on 27–29 Dec 2015, 15–17 Feb, 26–29 Mar. and 12 Apr. 2016. No surface water was noted on the raised plots. During these wet periods the crown of individual plants could be submersed in water for up to 48 h.

Table 7 Exp. 1. Mean dried biomass (g) for shoots, roots and flowers on harvesting after the second stress period. Treatments: CC = control, DD = double drought, WW = double waterlogging, DW = drought then waterlogging and WD = waterlogging then drought. For each taxon treatments with the same letter did not significantly differ (Games-Howell multiple comparison, $p < 0.05$). NB. Data for flower biomass was not sufficiently well-distributed to allow valid statistical comparisons

		CC	DD	WW	DW	WD
P. vulgaris	Shoots	5.2 [a]	5.0 [a]	4.7 [a]	3.8 [a]	5.4 [a]
	Roots	8.0 [ab]	6.4 [ab]	7.7 [ab]	5.1 [b]	9.0 [a]
	Flowers	0.1	0.0	0.0	0.0	0.2
P. 'Cottage Cream'	Shoots	3.0 [a]	2.8 [a]	3.0 [a]	2.9 [a]	2.8 [a]
	Roots	7.0 [a]	6.3 [a]	5.3 [a]	4.8 [a]	5.0 [a]
	Flowers	0.1	0.1	0.1	0.1	0.1
P. 'Alaska WOE'	Shoots	4.6 [a]	1.8 [b]	2.2 [b]	2.9 [b]	3.8 [ab]
	Roots	4.8 [a]	2.2 [b]	1.9 [b]	2.4 [b]	2.7 [b]
	Flowers	0.3	0.0	0.1	0.2	0.1
P. 'Forza'	Shoots	5.8 [a]	1.8 [ab]	0.5 [b]	1.8 [ab]	0.2 [b]
	Roots	2.3 [a]	1.1 [ab]	0.7 [b]	1.0 [ab]	0.2 [b]
	Flowers	2.7	0.7	0.1	0.7	0.0

Fig. 2 Exp. 2. Percentage fatalities in a range of *Primula* taxa over time after exposure to simulated control (C) or wet (W) winter (first letter), followed by a control (C), wet (W) or dry (D) spring/summer (second letter). Dashed line shows transition between winter and spring/summer regimes
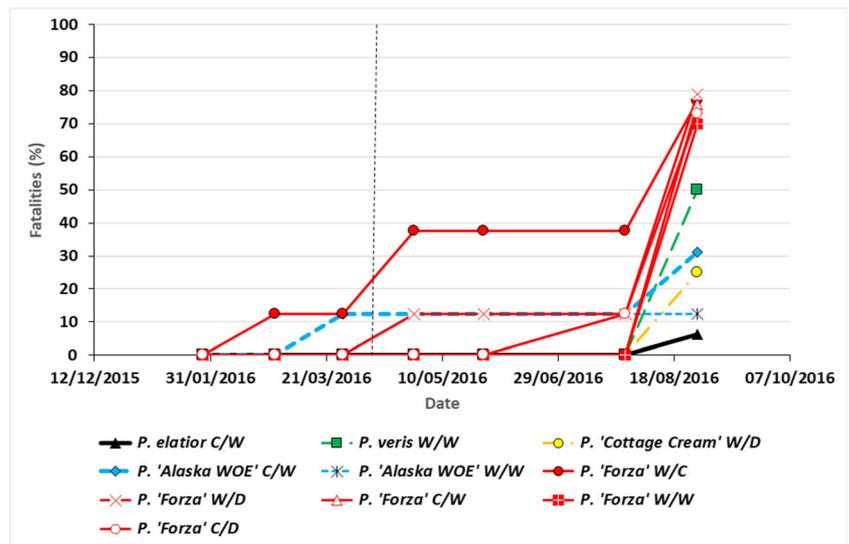
There was no evidence of treatment effects during the first spring (2015), but plant development the following year showed strong effects of both treatment and taxa (quality data for May 2016 is presented, Fig. 4). As before, *P. vulgaris* outperformed the cultivated forms (significantly so in the case of *P.* 'Alaska Orange' and *P.* 'Alaska Rose') with no loss of quality or size associated with any of the plot levels (Fig. 4, Table 9). In contrast, loss of quality in *P.* 'Alaska Blue' was greater with plants in sunken compared to raised plots. *Primula* 'Alaska Blue' in raised plots also performed significantly better than *P.* 'Alaska Rose' in any treatment (Fig. 4). *Primula* 'Alaska Orange' tended to be intermediate in its tolerance levels between the other two cultivars (differences NS). Flower score supported the other metrics of quality, with significantly higher numbers of flowers associated with *P. vulgaris* and lowest with *P.* 'Alaska Rose' (Fig. 5). By the end of the experiment (Jun. 2016) plant deaths were in the

order of; Sunken plots *P.* 'Alaska Rose' = 60%, *P.* 'Alaska Blue' = 10% and *P.* 'Alaska Orange' = 10% and in the raised plots *P.* 'Alaska Rose' = 50%.

Discussion

Climate change scenarios for Sheffield, UK were used to test the resilience of *Primula* species and cultivars to waterlogging stress, drought stress and combinations of the two. Data from semi-controlled experiments were augmented with resilience studies using plants in a real garden, but where raising or lowering the level of planting affected the degree of water available to plants. Of the taxa under study, *P. vulgaris* (the most widespread of the native species tested) demonstrated the greatest tolerance to hydrological stress. With the exception of the first drought phase in Exp. 1 (when loss of quality

Fig. 3 Exp. 2. Plant quality scores in a range of *Primula* taxa after exposure to simulated control (C) or wet (W) winter (first letter), followed by a control (C), wet (W) or dry (D) spring/summer (second letter). Data shows values at end of the experiment. Letters denote significant differences between treatments
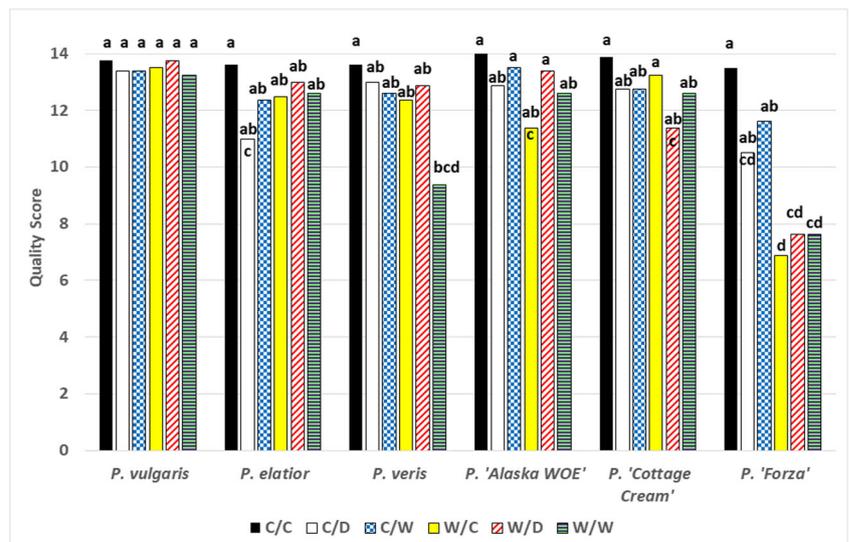
Table 8 Exp. 2. Estimated plant area (cm^2) of specimens of *Primula* taxa that survived treatments. Treatments relate to exposure to simulated control (C) or wet (W) winter (first letter), followed by a control (C), wet (W) or dry (D) spring/summer (second letter). Letters denote significant differences between treatments within a single taxon

	C/C	C/D	C/W	W/C	W/D	W/W
P. vulgaris	1388 [a]	1260 [a]	1377 [a]	1507 [a]	1572 [a]	1442 [a]
P. elatior	1217 [a]	881 [a]	1072 [a]	1212 [a]	1116 [a]	871 [a]
P. veris	1022 [a]	661 [ab]	628 [ab]	1040 [a]	518 [b]	866 [ab]
P. 'Cottage Cream'	780 [a]	545 [ab]	573 [ab]	655 [ab]	699 [ab]	412 [b]
P. 'Alaska WOE'	515 [ab]	444 [b]	408 [b]	722 [a]	419 [b]	417 [b]
P. 'Forza'	567 [ab]	448 [ab]	348 [ab]	689 [a]	551 [ab]	246 [b]

was comparable to *P.* 'Cottage Cream') *P. vulgaris* always out-performed all the cultivated forms of *Primula*. It was the only taxa to retain 100% survival, across all 3 experiments. Moreover, plants of this species often still performed well after periods of drought or waterlogging, showing the capacity to recover from stress, e.g. in terms of biomass accumulation (Tables 7, 8 and 9) or to produce good numbers of flowers (Fig. 5). As such, this species may have some capacity to survive and perform in garden settings despite the onset of a changing climate.

The research also revealed that there was variation in stress tolerance even within the cultivated forms of *P. vulgaris*. *Primula* 'Cottage Cream', which has the closest morphological resemblance to its parent species, surpassed the other cultivated varieties in stress tolerance. Whilst *P.* 'Cottage Cream' was negatively affected by stress in Exp. 1, it was the only cultivar to show signs of sustained recovery across all treatments, with final biomass not being different across treatments (Table 7). Additionally, notable differences were also observed in the performance of the two most highly-bred cultivars in Exp. 1 and 2, with *P.* 'Forza' exhibiting notably poorer performances and high mortality rates across all stress treatments than *P.* 'Alaska WOE'. Even within the one strain of *Primula* cultivars, i.e. Alaska, there was evidence that the blue flowered form (*P.* 'Alaska-Blue') coped better with periods of drying soil/drought (raised bed data) than the rose-coloured flower equivalent (*P.* 'Alaska-Rose') (Exp. 3, Fig. 4). Collectively, these results support the hypothesis that the species *P. vulgaris* has greater resilience to hydrological stress than its derived cultivated forms, and suggests that the process

of cultivation (breeding/selection) itself may result in trade-offs between garden performance and longer term viability. Indeed, subjectively the most flamboyant of the cultivars selected, i.e. *P.* 'Forza' proved to be the least resilient.

Do these results then suggest that the process of cultivation per se is a handicap, and that gardeners and other land managers should rely more on native species when dealing with the variability of a changing climate? The answer seems to depend on *which* native species. Not only did *P. vulgaris* out-perform its derived cultivars, it also showed more resilience in Exp. 2 to wet winter conditions than *P. veris* and dry spring conditions than *P. elatior*. Moreover, some cultivated forms of *Primula vulgaris* (*P.* 'Cottage Cream' and *P.* 'Alaska WOE') also performed equally well compared to these two species (e.g. Fig. 3). Thus, it cannot be guaranteed that any (native) species within the same genera will have more resilience than garden cultivated forms, despite the emphasis on the latter to have more ornamental traits (larger flowers and repeat flowering characteristics in this case). Therefore, we reject our second hypothesis that native species per se will necessarily out-perform cultivated plants within these climate change scenarios, just because they are have evolved to adapt to specific biotic and abiotic stress factors in natural, mixed plant communities.

Comparisons between the three species themselves, tend to confirm that *P vulgaris* has a wider hydrological ecological niche than either *P. veris* or *P. elatior* (Adamson 1912; Taylor and Woodell 2008; Jacquemyn et al. 2009). Potentially this wider ecological niche may help *P. vulgaris* tolerate the hydrological impacts of a changing climate better than the two

Table 9 Exp. 3. Estimated plant area (cm^2) of specimens of *Primula* taxa that survived treatments. Treatments relate to plants being planted at ground level, a raised bed or in a sunken depression within a garden situation. Letters denote significant differences between treatments within a single taxon. No values are depicted for *P.* 'Alaska-Rose' due to limited numbers of surviving plants in the raised and sunken beds

	Ground	Raised	Sunken
P. vulgaris	338 [a]	427 [a]	491 [a]
P. 'Alaska-Blue'	68 [b]	214 [a]	107 [ab]
P. 'Alaska-Orange'	61 [a]	115 [a]	115 [a]
P. 'Alaska-Rose'	45	77	42

Fig. 4 Exp. 3. Plant quality scores in a range of *Primula* taxa after being grown at ground level, within a raised bed or within a sunken depression in a garden situation. Letters denote significant differences between taxa/treatments
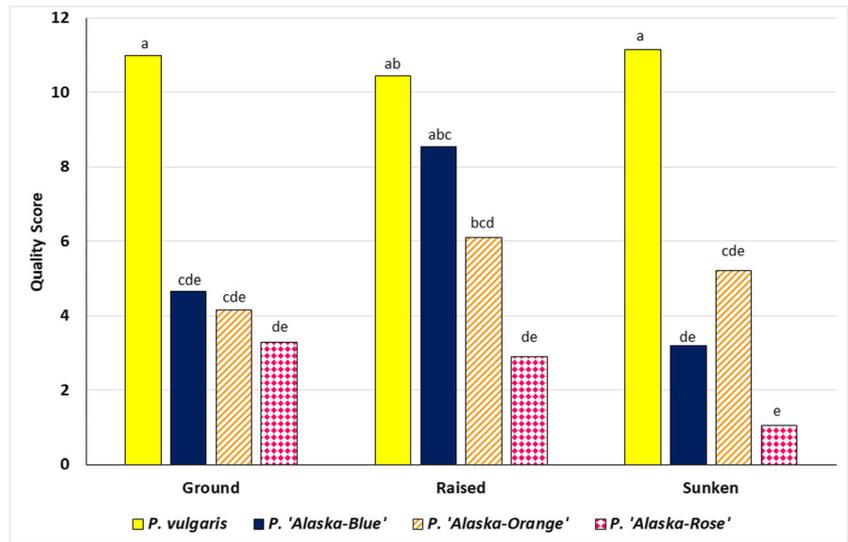

other species (Thuiller et al. 2005), as scenarios suggest both wetter and drier periods in future compared to the current climate. Although *P. elatior* generally performed well across all stress treatments (Exp. 2), lowest scores were observed in plants that experienced a standard (control) winter followed by a dry spring/summer (C/D). Whilst this difference was not significant, the trend is consistent with existing literature, which established that *P. elatior* was well-adapted to wet or waterlogged conditions but relatively intolerant of drought (Whale 1983). Similarly, *P. veris* also maintained high visual scores for the majority of the experimental period. However, the lowest scores were observed in plants that had experienced both a wet winter and a wet spring/summer, and this is consistent with a preference for a drier habitat as cited by previous literature (Whale 1983). This data is interesting, in that it suggests that even in the managed conditions of a garden, species with narrower ecological niches (dry-adapted etc.) may

themselves struggle to survive if conditions continue to diverge from those that they have become adapted to in natural settings. In effect, a changing climate may reduce the range of cultivated plants that can be grown in gardens, but also reduce the palette of native and near native species that can be utilised if these themselves are not resilient enough to cope with oscillating water availability.

The scenarios developed in this research exposed plants to both over-wetting and excessive soil drying, but was one of these stress factors more critical than the other for the cultivated *Primula*? The data demonstrated there was some variation in the relative susceptibilities to drought and over-watering in the cultivated forms, although trends were not always consistent. There was evidence that in Exp. 1, *P.* 'Cottage Cream' and *P.* 'Alaska WOE' (as well as *P. vulgaris*), when exposed to the initial drought, experienced a pronounced drop in visual quality and photosynthetic

Fig. 5 Exp. 3. Flower scores (mean numbers per plant recorded Mar-May, 2017) in a range of *Primula* taxa whilst grown at ground level, within a raised bed or within a sunken depression in a garden situation. Letters denote significant differences between taxa/treatments
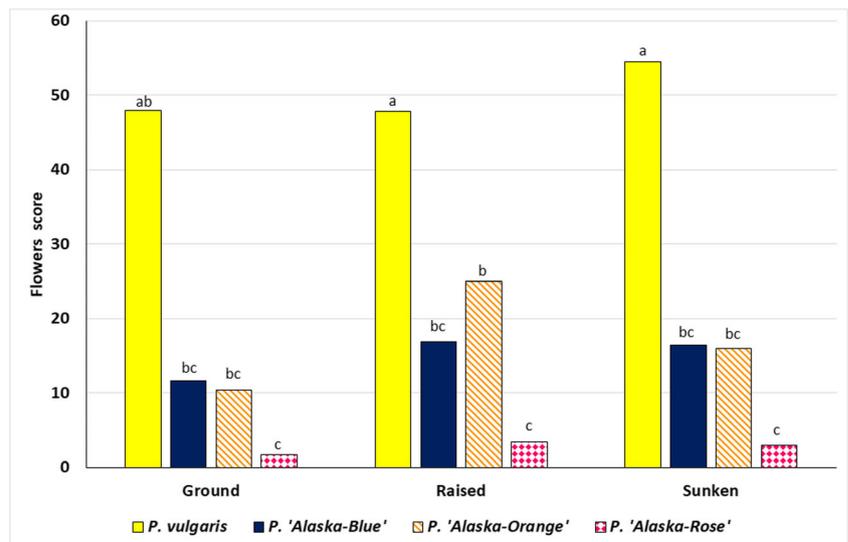
performance. However, these impacts appeared to be rapidly reversed upon re-watering. Conversely, data suggested that *P.* Forza (Figs. 2 and 3), *P.* 'Alaska WOE' (Table 5) and *P.* 'Alaska Blue' (Fig. 4) particularly resented waterlogging. In *P.* Forza, waterlogging in cool winter months was detrimental, despite the concept that the impacts of waterlogging are worse at warmer temperatures due to accelerated depletion of oxygen in the rhizosphere under such conditions (Jackson and Ricard 2003; King et al. 2012).

Data on biomass accumulation reflected trends in plant performance, with greatest differentials in weight between controls and stressed plants associated with the more highly-cultivated taxa. Notably too, the varieties that fared better under stress in Exp. 1 (i.e. *P. vulgaris* and *P.* 'Cottage Cream') allocated a greater proportion of their total biomass to roots. Anecdotally, these taxa also appeared to limit flowering after the initial stress exposure, a trend not apparent in the highly-cultivated forms.

Collectively, these results add weight to the suggestion that altering plant phenotype to favour traits of human interest is not without cost in biological terms and can ultimately impact the performance of the plant as a whole. This may be apparent even in designed and intensively-managed landscapes, where conditions are modified through routine addition of fertiliser and water, alongside the reduced impacts of competition from weeds. These costs likely stem from trade-offs, which arise due to the proportional allocation of limited resources across energetically demanding traits (Mole 1994; Koenig et al. 2013). Looking at the response of unstressed plants suggests that the increased investment in floral biomass observed in *P.* 'Forza', e.g. at the expense of root biomass (Table 7) was most likely the result of re-distribution of resources, rather than an increase in productivity. This observation is consistent with trends recorded in agricultural crops (Evans 1996), and may in part explain the poor stress tolerance of this cultivar.

The development of cultivars under the intense management, resource-rich, low stress environment normally associated with cultivation (Denison 2012) may also have altered trait profiles (Milla et al. 2015). A well-established tenet in the ecological literature, suggests that nutrient rich environments promote selection of species (or individuals) with acquisitive trait profiles (Chapin 1980; Reich 2014). Consequently, as cultivated environments are generally nutrient rich, it may be reasonable to suggest that cultivars are more likely to express phenotypes with acquisitive trait profiles. Whilst such traits (e.g. vigorous growth) may be favourable in cultivation they are not commonly associated with stress tolerance (Grime 1977). As such the process of cultivation (i.e. promoting plants that rely on rapid acquisition of resources and then exploiting these for 'luxuriant' shoot/leaf growth and high flower production) may result in reduced stress tolerance, leaving these cultivars vulnerable to the predicted increases in hydrological stress.

From a gardener's perspective this research suggests that both the natural distribution (for the species, e.g. Broennimann et al. 2006; Yu et al. 2017) and the visual degree of cultivation (for the cultivars) provide effective tools to predict genotype response to stress. Species with wide natural distributions are typically generalists, and often maintain 'performance' over a variety of hydrological conditions (Lieffers et al. 2001; Zaharieva et al. 2004; Gratani 2014), thus making them attractive for garden use. Therefore, gardeners wishing to achieve a 'climate resilient' garden should consider wild species or the less highly-bred genotypes, as these appear more resilient than more flamboyant, highly-cultivated taxa. However, this research has focused on a small number of *Primula* taxa. Whilst results have been consistent across both controlled experiments and outdoor trials, it is advisable to test these assumptions on other species to determine whether trends are more broadly applicable.

Nevertheless, this data on *Primula* acts as a precedent. If many cultivated forms of garden/landscape plants prove to have limited resilience to a changing climate, the implications for designed landscapes are significant. Gardens constitute 15–25% of the urban landscape (Gaston et al. 2005), underpin a wide range of ecosystem services (Cameron et al. 2012; Cameron and Blanuša 2016) and contribute significantly in economic terms; e.g. one-third of tourists to the UK (an industry worth £7.8bn pa) will visit a garden during their stay (Smithers 2013). The inability to maintain cultivated plants will reduce garden flora diversity, and impact on the popularity of heritage gardens (Bisgrove and Hadley 2002; Webster et al. 2017). Moreover, many private gardeners may lose interest, due to a depopulate range of plant taxa available commercially (novel cultivated plant lines are a principle driver for nurseries and garden centres to remain profitable, and attracting return custom from 1 year to the next; Hobbs pers. comm.). Correspondingly, this research suggests that ornamental plant breeders should give more emphasis to enhancing stress tolerance in new cultivars, when considering/ prioritising desirable traits (Kuligowska et al. 2016). Strategies should be developed to ensure new genotypes are introduced that retain attractive flower colours and shapes, whilst not compromising on their capacity to tolerate a range of abiotic stresses. Failure to do so, may simply result in the loss of our iconic, florally-diverse gardens – perhaps in itself, a metaphor for a globally-changed climate!

Conclusions

Cultivars dominate many designed landscapes including public and private gardens. Despite this, relatively little is known about their ability to tolerate the hydrological extremes that are likely to become more frequent in the near future. Our research in both controlled and garden experiment settings

found strong evidence to suggest that highly-cultivated taxa of *Primula* are more susceptible to extreme stress (including both waterlogging and drought). If many cultivated forms of garden/landscape plants prove to have limited tolerance to the effects of climate change (such as more radical oscillations in soil moisture availability), even when maintained in highly-managed landscapes, then the implications are significant. The loss of a high proportion of cultivated plants (and as this paper also implies, less generalist species) from gardens and parks would have an immense impact on the floral diversity of such landscapes, and in terms of public/heritage gardens undermine the viability of many. Thus a key consequence of this research is a call for ornamental plant breeders to give much greater consideration to stress tolerance when breeding and selecting new cultivars.

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