Received: 30 August 2023 | Accepted: 24 April 2024

DOI: 10.1111/wre.12633

ORIGINAL ARTICLE

WEED RESEARCH An International Journal of Weed Biology, Ecology and Vegetation Management

WILEY

Potential importance of vegetative spread and fragment regeneration for invasiveness of *Clematis vitalba*

Brenda Jarvis-Lowry | **Kerry C. Harrington** | **Hossein Ghanizadeh** | **Alastair W. Robertson**

School of Agriculture and Environment, Massey University, Palmerston North, New Zealand

Correspondence
Alastair W. Robertson, Ecology & Zoology Group, School of Food Technology & Natural Sciences, Private Bag 11222, Massey University, Palmerston North 4442, New Zealand.
Email: a.w.robertson@massey.ac.nz

Funding information
New Zealand Tree Crops Association; George Mason Charitable Trust; New Zealand Biosecurity Institute; New Zealand Plant Protection Society; Horizons Regional Council; Massey University Seed Tech Services

Subject Editor: Stephen Novak; Boise State University; Boise; USA

Abstract

Identifying characteristics of invasive species or growth forms that facilitate their range expansion is critical for management. *Clematis vitalba* L. (old man's beard) is an invasive temperate liana in many areas of its introduction, yet its seedlings do not thrive in circumstances where resources are limited. Although some lianas in both tropical and temperate climates have been shown to spread by clonal stems along the ground, the bulk of previous research on *C. vitalba* reproduction has focused largely on aspects of seed ecology. The vegetative growth of the species is poorly understood. The first objective of our study was to evaluate the use of vegetative spread by *C. vitalba* as a means of local dispersal and population growth. We excavated ten 1-m^2 plots in infested riparian zones and found an extensive, branching network of creeping stems, both above and below ground. Our second objective was to test the ability of *C. vitalba* stem fragments to act as vegetative propagules. After 4 months, ~50% of two-node fragments had regenerated, from both creeping and climbing stems. These studies help explain how a temperate liana forms populations and dominate ecological communities. The findings provide good evidence that *C. vitalba* may rely quite heavily on asexual reproduction. In addition, the results document liana stem phenotypic plasticity; fragmented climbing stems are just as likely as fragmented creeping stems to reprogram shoot tissue systems, generate roots and regrow as independent plants.

KEYWORDS
asexual reproduction, clonality, liana, old man's beard, plant regrowth, temperate, woody invasive

1 | INTRODUCTION

Successful dispersal, recruitment of new plants, and maintenance of a reproducing population are all elements of a successful invasive plant species (Davis, 2009). Employing multiple mechanisms to those ends improves the chances of a favourable outcome. Indeed, in addition to reproduction by seed, some lianas in both tropical and temperate zones, including invasive species, rely at least partly on vegetative growth (growth that involves non-flowering plant parts) for dispersal, recruitment, and reproduction (Buru et al., 2016;

Larson, 2000; Leicht-Young & Pavlovic, 2015; Mori et al., 2020; Penalosa, 1984).

The main benefit of sexual reproduction is that it ensures genetic diversity in a population, which leads to adaptability in changing environments. As a complementary system, vegetative reproduction generally supports more rapid growth and range expansion with fewer resource inputs than sexual reproduction (Schurko et al., 2009). Lianas can produce multiple stems, which elongate and branch, root, and develop shoots, both on the ground and as climbers, which enables short-distance expansion. Pollinators and mates for cross-fertilisation are unnecessary for such growth. Thus, it is possible for a single successful, genetically fit seedling or plant fragment to arrive and populate a new habitat by vegetative spread.

When vegetative plant parts that form adventitious roots are subsequently separated from the mother plant (genet), they become independent clones (ramets) of the genet (Jeník, 1994; Munné-Bosch, 2015; Oborny & Bartha, 1995). Another form of clonal reproduction is through the regeneration of plant parts into individual ramets after fragmentation (Mogie & Hutchings, 1990). Ramets represent new recruits, which increase propagule pressure and a plant's odds of surviving in a new environment because the risk of destruction is reduced with the presence of more individuals (Colautti et al., 2006; Davis, 2009; Richardson et al., 2007).

For a plant species that is incapable of growing upright on its own, the optimal circumstance is to climb a tree or other support, which allows it to maximise its photosynthetic capacity. Ground-based vegetative spread permits an established liana to expand its range, albeit incrementally, while searching for trees to support its stems (Wyka et al., 2019). Research has shown that many species of creeping lianas can produce dense networks of branching stems, both above and below ground (Buru et al., 2016; Leicht-Young et al., 2011; Putz, 1984; Sakai et al., 2002; Schnitzer et al., 2000). The creeping stems root at the nodes, which physically anchor them to the ground and provide an increased uptake of water and soil nutrients. As discussed above, rooted fragments that become severed from the rest of the stem can become self-sufficient plants, yet any connections between the rooted nodes allow them to share resources and enhance their resiliency in less-than-ideal environments (Marshall, 1990; Roiloa et al., 2014). The connections also make it possible for any shoots and leaves along the continuum to provide photosynthates to other sections of the stem. Furthermore, the active and dormant buds on vegetative growth serve as a "bud bank" (Ott et al., 2019), complementary to the seed bank a liana may develop, to allow the species to persist over time.

Clematis vitalba L. (old man's beard) is a very troublesome non-native liana in some native forest remnants (Ogle et al., 2000). Although new research has demonstrated poor survivability of very young *C. vitalba* seedlings in the presence of dense ground cover (Jarvis-Lowry, 2023), in New Zealand, more mature vines have been reported to grow at a rate of 6.3 kg m^{-2} yr^{-1} (fresh weight), using twining petioles to climb and smother trees and shrubs indiscriminately (West, 1992). Recent rudimentary investigations indicate that *C. vitalba* could also become problematic in non-native farm forestry settings in New Zealand, where site preparation between rotations and before planting tree seedlings involves mechanically breaking and clearing debris with bulldozers and stacking into windrows, including any *C. vitalba* that may be present. Evaluation of small *C. vitalba* individuals at a *Pinus radiata* plantation forest in Taihape, New Zealand, suggested that nearly all shoots arose, not from true seedlings, but from creeping stems that appeared to originate in the windrows between the trees, indicating that broken stem fragments had regenerated (personal observations, December 2019).

Clematis vitalba may rely heavily on vegetative growth and reproduction, yet there has been no peer-reviewed research published on the ability of the species to asexually reproduce. Two New Zealand studies: (1) an unpublished government report (referenced by Kennedy, 1982); and (2) a master's thesis (Van Gardingen, 1986), have examined the capacity of *C. vitalba* stem fragments to regenerate. In April while the plant was going dormant, Van Gardingen (1986) collected two-node fragments from a mature vine, placed them upright in 1:1 mix of sand and loam, with one node covered, and watered overhead. Monitored over the course of 8 months, there was no growth of any kind. Kennedy (1982) mentioned that McClelland reported poor regeneration from one-node sections but found that 20% of fragments from stems that were at least 3 years old produced shoots. Only 12.5% of 2-year-old fragments regenerated, and no younger material regenerated. Few other details are known about either of these studies. To the best of our knowledge, vegetative spread in *Clematis vitalba* has not been studied outside of New Zealand.

Temperate lianas are not as well-studied as those in tropical regions (Ladwig & Meiners, 2015; Mori et al., 2018). The purpose of this study was to discover what role vegetative growth may play in the invasion success of *C. vitalba*, with two objectives: (1) determine the extent of vegetative spread in creeping stems of *C. vitalba*; and (2) determine how readily *C. vitalba* stem fragments (from both creeping and climbing stems) can regenerate. To this end, an initial in situ observational study was carried out to investigate the frequency of natural layering and branching of *C. vitalba* creeping stems as potentially important contributors to dispersal, recruitment, and survival of the species. Based on these observations, an ex situ experiment was designed to test the ability of *C. vitalba* stem fragments to act as vegetative propagules after injury. As the first steps in characterising and defining the magnitude of its vegetative reproduction, these results may help predict the spread of *C. vitalba*, inform choices for its control, and contribute to understanding temperate liana ecology.

2 | MATERIALS AND METHODS

2.1 | In situ observations

In January–February 2021 (mid-late summer), three river flood plain sites in the Manawatu Region, New Zealand (Manawatu River at Awapuni [−40.3861, 175.5858], Oroua River at Awahuri [−40.2763, 175.5208], and Rangitikei River near Halcombe [−40.1238,

175.4458]), each separated by at least 17 km were selected as representative of riparian zones highly infested with *C. vitalba*. Across the three sites, a total of 10 random 1 m × 1 m plots (five at Awapuni, two at Awahuri, and three at Halcombe) were chosen, all at least two metres from the nearest tree (only creeping stems were present in the plots, unsupported by any sort of trellis). The plots were excavated by hand to determine the characteristics, abundance, and frequency of rooting, branching and shoot development of the *C. vitalba* stems present, both above and below the soil surface. All *C. vitalba* material inside the boundaries of the plot was examined, whether it grew into the plot from outside or was rooted in the plot. Any portion of stems or shoots that extended beyond the plot boundaries was excluded. Plots represented a range of vegetation cover of the study species, from approximately 10% to 90%. Shade levels in the plots from overhead trees ranged from 10% to 75% of full sunlight; the canopy cover index (immediately above the ground level vegetation) of each plot was calculated using the Gap Light Analysis Mobile Application (GLAMA) for Android phones (Tichý, 2019; see Table S1). All vegetation other than *C. vitalba* within each plot was removed, and all *C. vitalba* stems and associated parts were traced to their lowest point underground (Figure 1), removed, examined and measured (stems and shoots were stretched linearly and measured in a straight line to the meristem). In each plot, the following was recorded: (1) whether stems were found above or below the soil surface; (2) depth of stems below soil surface; (3) diameter of stems present; (4) presence of stem branching; (5) the distance between stem nodes; (6) number of nodes with roots; (7) number of nodes with shoots (current year's new stems); (8) any flower or achene production from creeping shoots; (9) length of stems and shoots.

2.2 | Ex situ experiment

To obtain material at an optimum time for re-growth, stem fragments for this experiment were collected just as the first spring flush of *C. vitalba* growth began (mid-September 2021, early spring). Woody stem fragments of both climbing and creeping stems were collected from the same three sites where the in situ observations were conducted. Eighty fragments of each stem type were obtained and cut to 30 cm in length, with two nodes. Visible bud activity at the nodes (leaves/shoots or roots) and fragment diameter (which ranged from 2 mm to 2.5 cm) were recorded.

Regeneration begins with adventitious rooting, which is contingent on numerous factors, including appropriate environmental conditions, an appropriate balance of endogenous compounds, and an inherited ability to allow differentiated cells to de-differentiate and form new tissue (Geiss et al., 2009). No attempt was made in this experiment to manipulate any endogenous factors, although environmental conditions were optimised for rooting of *C. vitalba* stem fragments. Immediately following collection, the fragments were placed at random in punnet trays and covered completely with soil-less potting mix with a controlled-release fertiliser (see Data S1 for additional details). Trays were kept in a shade house (45%–50% full sunlight), with no supplemental light, but with regular hand weeding and daily

FIGURE 1 Left: Plot (1 m^2) staked and edges cut; Right: Following removal of all non-target species vegetation, all above and belowground *Clematis vitalba* stems removed (30 cm deep). The prominent white flowers in the right-hand image belong to another creeping species, *Calystegia silvatica* (Kit.) Griseb. ssp. *disjuncta* Brummitt.

overhead watering. The maximum daily temperature ranged from 19.3°C in September to 27.3°C in January. Four months after burial (January), fragments were removed from the trays. As a measure of regeneration, the presence of any nodal growth and the number and length of shoots at each node were recorded.

2.3 | Data analysis

The observational study was an exploratory investigation of the horizontal stem morphology and growth patterns of *C. vitalba*, and due to the limited number of plots assessed (each plot took an average of 4 h to excavate), no statistical analysis was undertaken.

Analysis of the ex situ experiment was carried out using R statistical software, version 4.2.0 (R Core Team, 2022). Due to the time required to dig up belowground stems, 90% of the creeping stems were obtained from above ground. To avoid bias from unbalanced sampling, belowground stems were eliminated from the analysis. Prediction of stem regeneration and yield (number of shoots produced by fragment) was made by fitting a negative binomial regression model, with the MASS package (Venables & Ripley, 2002). Stem type (creeping or climbing), initial stem diameter, and initial presence of an active bud (whether root or shoot) were included as fixed effects. Also, a linear regression mixed model was fitted to predict the total length of new shoots produced, with the lmerTest package (Kuznetsova et al., 2017). Stem type and initial stem diameter were included as fixed variables, with tray as a random variable. For the linear model, assumptions of normality and heterogeneity of variance were violated, so a standardised square-root transformation was performed on the data before fitting the model (the most appropriate transformation was calculated using the bestNormalize package; Peterson, 2021).

To achieve a non-singular fit, stem provenance was not used as a variable in either model. As no interaction terms were significant in either model, models of main effects were selected based on Akaike Information Criterion (AIC) and goodness of fit calculated with the DHARMa package (Hartig, 2022). Multicollinearity of fixed predictors was calculated using the variance inflation factor (VIF) with the car package (Fox & Weisberg, 2019), and visualisation of the model was accomplished with the effects (Fox, 2003) and ggplot2 packages (Wickham, 2016).

3 | RESULTS

3.1 | In situ observations

In the 10 study plots, *C. vitalba* was found to have a complex lateral network of stems, roots, and shoots. No more than 20% of stems were found below ground, up to a median depth of 25 cm. Median diameter of belowground stems was 5.2 mm (interquartile range [IQR] = 4.40, 6.45) and of aboveground stems was 4.0 mm (IQR = 3.20, 4.90; Figure 2). Median branching frequency of aboveground stems was once per metre (1.03; IQR = 0.84, 1.16), and belowground stems every 0.44 m (IQR = 0.10, 0.61). Nodes were produced every 10–16 cm in all stems, with roots present at fewer than 1% of aboveground nodes (median 0.49; IQR = 0.26, 0.57) but at 67.5% of belowground nodes (IQR = 60.25, 93.50). Shoots were present at 11.2% of belowground nodes (IQR = 8.50, 13.92) and of 30.4% aboveground nodes (IQR = 22.72, 38.27). Most shoots were produced at nodes with roots present, and often multiple shoots were present at a single node. No seedlings were found in any of the plots investigated; all small 'individuals' were actually shoots originating from a creeping stem. In 60% of plots, no flowers were present, but in the remaining plots, 3.35% of shoots produced by aboveground stems had also produced flowers or flower buds. In the plots with 80%–90% *C. vitalba* cover, a 1 m^2 plot yielded 42–48 m of older (earlier than current year) stems (16 m belowground, 29 m aboveground) and 80–94 m of young, leafy shoots (the current year's stems).

3.2 | Ex situ experiment

Four months after collection, 48.7% of all stems (48.0% of creeping stems and 49.4% of climbing stems) had produced new shoots and roots. All new growth originated from the nodes (32% of all nodes: 30% of creeping stem nodes and 34% of climbing stem nodes). Of those stems that had at least one visibly active bud (roots or shoots present) at the time of fragmentation and burial, 50.7% regenerated, whereas 47.7% of stems with no active initial bud regenerated. Neither stem type nor the presence of an active bud at the time of fragment collection were significant predictors of fragment regeneration or regrowth yield (stem type $p = 0.99$; active bud $p = 0.97$). On the other hand, for every 1 mm unit increase in initial diameter, the expected count of shoots produced in the 4 months following fragmentation increased by 85% (incident rate ratio [IRR] = 1.849, $p = 0.02$: Table 1, Figure 3).

Total new shoot length per 30 cm stem fragment averaged 61 cm, but neither initial diameter nor stem type were important predictors of shoot length at $\alpha = 0.1$ at that early stage of regeneration (Table S2). An additional observation of note was the development of flower buds on shoots from three stem fragments, two climbing and one creeping. All three fragments measured between 3 and 5 mm in diameter at the time of collection.

4 | DISCUSSION

4.1 | In situ observations

Creeping *C. vitalba* stems were pervasive in highly infested sites, forming an intricate, branching web of vegetative growth at the ground level. The measurements and observations made from the excavated plots give a good indication that *C. vitalba* relies quite heavily on creeping vegetative growth. This is consistent with research on other liana species, many of which have clonal tendencies

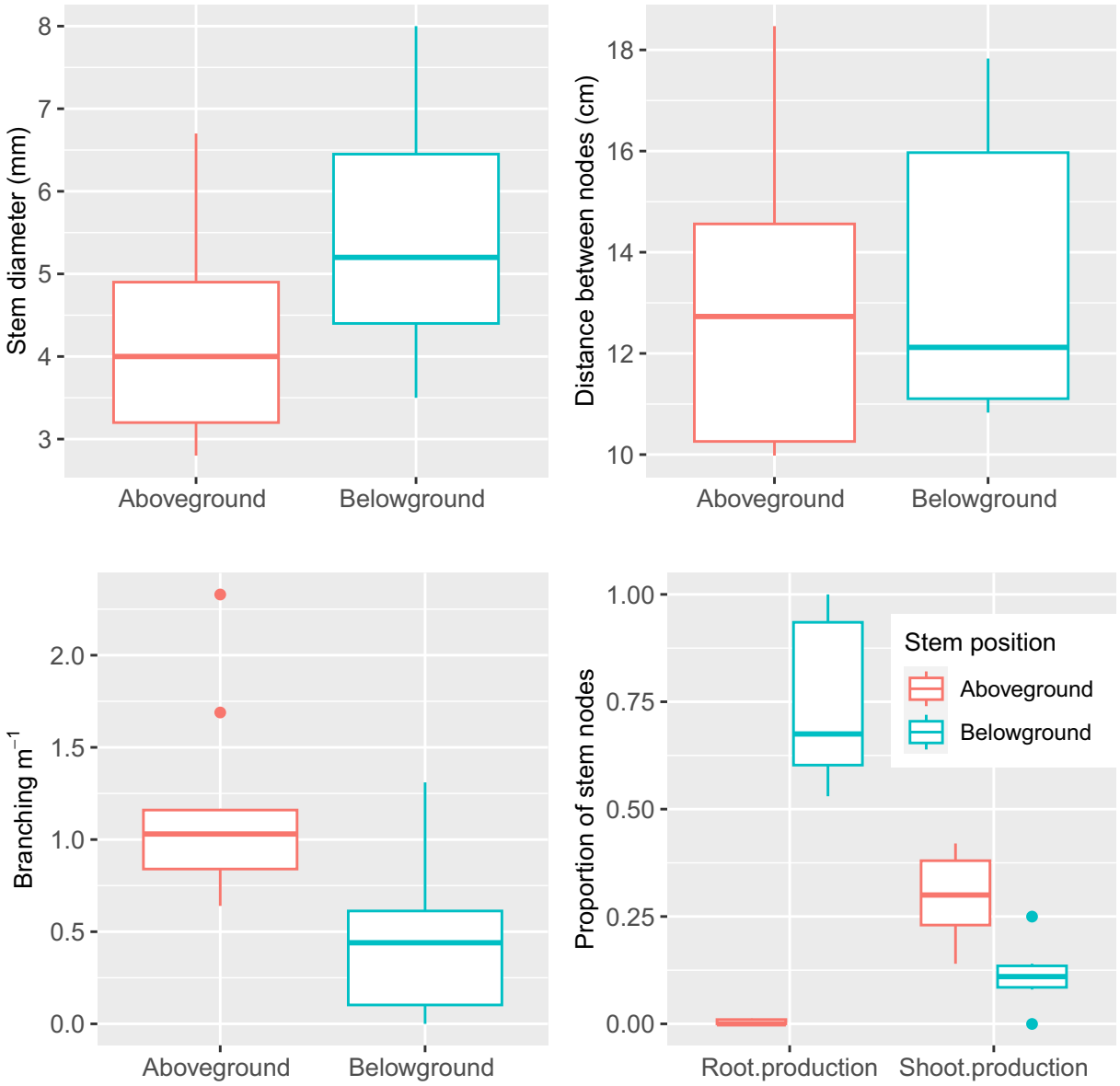

FIGURE 2 Data from excavation of *Clematis vitalba* stems in 1 m^2 plots in infested riparian zones, comparing differences between above and belowground stems. Clockwise from top left: boxplots comparing stem diameter; comparison of distance between stem nodes; comparison of stem branching frequency; proportion of stem nodes producing roots, and proportion producing shoots.

TABLE 1 Coefficient estimates and incidence rate ratios (IRR) from a negative binomial regression model (selected based on AIC and goodness of fit diagnostics using DHARMa package in R) factor effects on the regeneration (number of shoots produced) of 30 cm, 2-node *Clematis vitalba* fragments.

Predictors	Estimate (SE)	Est CI	*p*	IRR
(Intercept)	−0.130 (0.345)	−0.862, 0.626	0.706	0.878
Initial fragment diameter	0.615 (0.271)	0.085, 1.193	**0.023**	1.849
Active initial bud	−0.012 (0.279)	−0.589, 0.570	0.965	0.988
Vertical stem[a]	−0.004 (0.277)	−0.581, 0.569	0.990	0.996
Observations	149			

Note: The *P*-values in bold are significant at $\alpha = 0.05$.
[a]Vertical, climbing stems (as opposed to lateral, creeping stems).

(Buru et al., 2016; Leicht-Young & Pavlovic, 2015; Mori et al., 2018; Penalosa, 1984; Sakai et al., 2002). Aboveground stems comprised more than 80% of the lateral network, and in all the plots examined, no true seedlings were found. However, it is worth noting that the ground in these sites had a heavy vegetation cover with no bare soil, and therefore true seedlings would not likely have survived there due to poor survivability of *C. vitalba* seedlings in such situations (Jarvis-Lowry, 2023).

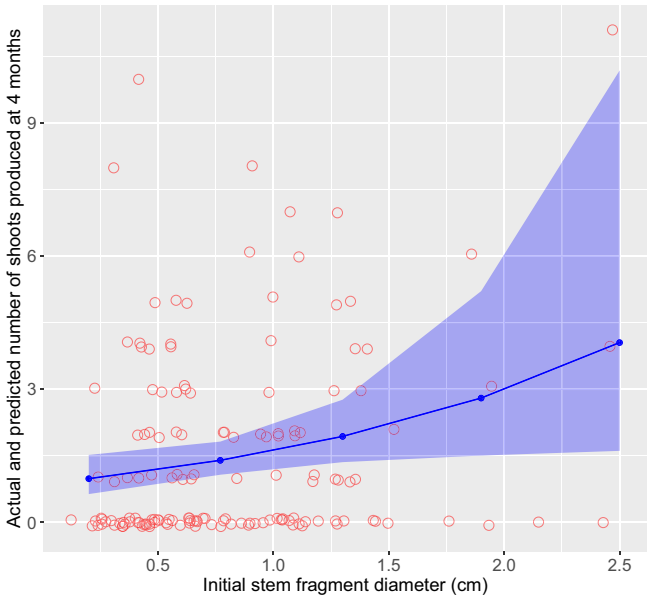

FIGURE 3 Negative binomial regression modelled probability of fragmented *Clematis vitalba* stems regenerating (indicated by number of shoots produced), as a function of initial stem diameter. Red data points are observed values, blue line and blue 95% confidence band are model estimates.

West (1992) documented vigorous and rapid elongation of *C. vitalba* shoots in New Zealand, and found average shoot elongation in one season to be just over 2 m. As a validation of that vigour, in the plots with the highest density of the target species, the length of shoots generated by the stems (>80 m) was double that of the stems themselves (>40 m).

A small fraction of shoots (<3%) from the creeping stems bore buds or flowers at the time of the observational study, which was during the middle of the phenological flowering period for *C. vitalba* (West, 1992). Hence, creeping stems can support sexual reproduction as well as vegetative growth. However, the primary function of aboveground stems is apparently to produce photosynthetically active growth (26% of nodes) while elongating, with only a small investment in rooting (5.5% of nodes). On the other hand, belowground stems seem to primarily function as conduits for water and nutrients: nearly half of belowground stem nodes developed roots (44.8%), whereas only 7% produced shoots.

4.2 | Ex situ experiment

Clematis vitalba stems climb by wrapping twining petioles around suitably sized supports. No published descriptions of climbing *C. vitalba* stems refer to adventitious rooting, nor have inspections of vertical stems by the researchers produced any evidence of rooting (personal observations, 2019–2022). Accordingly, any active buds on climbing stems would have been forming shoots and leaves or had a bud with a potential shoot system at the time of collection, but no roots (Hartmann et al., 2018). In the observational study, only 1% of aboveground creeping stem nodes developed adventitious roots under normal circumstances, while over 30% of the same nodes produced shoots. Consequently, because only aboveground creeping stem fragments were used in the study, they would not have been much more likely than climbing stems to recover from fragmentation by rooting. The study findings confirmed that whether woody *C. vitalba* fragments originated from creeping or climbing stems, they had the same propensity in optimal conditions to grow roots and regenerate (48.7%). Previous research (Ward & Henzell, 2000) found that *C. vitalba* stems that were cut down but left rooted resulted in 61% regrowth when pruned in late spring. The current experiment shows that spring-fragmented stems removed entirely from their original habitat were slightly less successful at regenerating than those spring-cut stumps that were still firmly rooted in the ground. This result indicates that buds on the fragments were readily able to convert potential leaf and stem tissue to root tissue for regeneration (Geiss et al., 2009; Su et al., 2021).

Although highly variable between species, plastic reprogramming of tissue is a well understood aspect of clonal plants and has been widely exploited in plant propagation practices (Hartmann et al., 2018; Kevers et al., 2009; Tailor et al., 2022). This same plasticity was also reflected in the morphological differences observed between the above and belowground stems of the in situ study. Many tropical lianas have been shown to fall with their hosts, develop adventitious roots and spread along the ground in search of a new host (Putz, 1984; Schnitzer et al., 2000; Schnitzer et al., 2004; Yorke et al., 2013). Given that *C. vitalba* in the canopy can cause the death and collapse of host trees, its dynamic plasticity should easily permit *C. vitalba* stems that drop with the host to behave similarly, whether the stems remain attached to the mother plant or become fragmented.

Researchers have typically documented a *loss* of ability to form adventitious roots as a plant ages, though the decline varies by species (Díaz-Sala et al., 2002; Greenwood et al., 1989; Horstman et al., 2017). Although vertical and lateral stems were equally capable of regrowth in this study, the results suggest larger diameter *C. vitalba* fragments have a significantly better chance of successfully forming independent ramets than their smaller counterparts. Fragment diameters ranged from 2.0 mm to 2.5 cm in the current experiment. Certainly, annual secondary growth depends on environmental conditions, and stem age cannot be precisely determined based solely on diameter. Nonetheless, several 2 cm *C. vitalba* stem cross sections observed by the lead author had 8–10 annual rings (personal observations, 14 January 2021). Thus, rooting capacity of *C. vitalba* is likely to increase with age but requires further investigation.

4.3 | Management implications

The results of this research indicate that in a forestry plantation or other environments where land is cleared mechanically, each metre of *Clematis vitalba* stem broken up by machinery in spring could yield several new, independent plants, each with multiple shoots. Flower production can occur in the first year from a regenerated stem fragment, and hence both asexual and sexual propagation are possible in

the same year as the clearing. Thus, mechanical clearing into windrows could exacerbate an infestation, unless *C. vitalba* growth from the windrows is repeatedly controlled. Removal of all stems would be a preferable alternative, although considering the extensive nature of creeping stem networks, full removal may be impractical where infestations are severe unless they can be sprayed prior to winter dormancy and mechanical clearance.

ACKNOWLEDGEMENTS

Financial support for this research was given by Massey University, Horizons Regional Council, New Zealand Plant Protection Society, New Zealand Biosecurity Institute, George Mason Charitable Trust, New Zealand Tree Crops Association, and Massey University Seed Tech Services. Thanks to Lesley Taylor, Su Liu, and Sunil Sapkota for their technical help. Open access publishing facilitated by Massey University, as part of the Wiley - Massey University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/wre.12633.

DATA AVAILABILITY STATEMENT

Data are available from the Open Science Framework Repository (Jarvis-Lowry B, Harrington KC, Ghanizadeh H, Robertson AW. 2024. Potential importance of vegetative spread and fragment regeneration for invasiveness of *Clematis vitalba*. osf.io/tdn84).

ORCID

Brenda Jarvis-Lowry https://orcid.org/0009-0008-0595-626X
Kerry C. Harrington https://orcid.org/0000-0003-2238-516X
Hossein Ghanizadeh https://orcid.org/0000-0001-5381-7880
Alastair W. Robertson https://orcid.org/0000-0001-6894-2158

REFERENCES

Buru, J.C., Dhileepan, K., Osunkoya, O. & Firn, J. (2016) Comparison of growth traits between abundant and uncommon forms of a non-native vine, *Dolichandra unguis-cati* (Bignoniaceae) in Australia. *NeoBiota*, 30, 91–109. Available from: https://doi.org/10.3897/neobiota.30.8495

Colautti, R.I., Grigorovich, I.A. & MacIsaac, H.J. (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions*, 8(5), 1023–1037. Available from: https://doi.org/10.1007/s10530-005-3735-y

Davis, M.A. (2009) *Invasion biology*. New York: Oxford University Press.

Díaz-Sala, C., Garrido, G. & Sabater, B. (2002) Age-related loss of rooting capability in *Arabidopsis thaliana* and its reversal by peptides containing the Arg-Gly-Asp (RGD) motif. *Physiologia Plantarum*, 114(4), 601–607. Available from: https://doi.org/10.1034/j.1399-3054.2002.1140414.x

Fox, J. (2003) Effect displays in R for generalised linear models. *Journal of Statistical Software*, 8(15), 1–27. Available from: https://doi.org/10.18637/jss.v008.i15

Fox, J. & Weisberg, S. (2019) *An R companion to applied regression*, 3rd edition. Thousand Oaks, CA: SAGE Publication.

Geiss, G., Gutierrez, L. & Bellini, C. (2009) Adventitious root formation: new insights and perspectives. In: Beeckman, T. (Ed.) *Annual plant reviews. Volume 37: Root development*. Chichester, West Sussex: Wiley & Sons, pp. 127–156.

Greenwood, M.S., Hopper, C.A., & Hutchison, K.W. (1989) Maturation in larch: effect of age on shoot growth, foliar characteristics, and DNA methylation. *Plant Physiology*, 90(2), 406–412. Available from: https://doi.org/10.1104/pp.90.2.406

Hartig, F. (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models (version R package version 0.4.5). Available from: https://CRAN.R-project.org/package=DHARMa [Accessed 11th August 2022].

Hartmann, H.T., Kester, D.E., Davies, F.T., Jr., Geneve, R.L. & Wilson, S.B. (2018) Principles of propagation by cuttings. In: *Plant propagation: principles and practices*, 9th edition. Upple Saddle River, NJ: Pearson.

Horstman, A., Li, M., Heidmann, I., Weemen, M., Chen, B., Muino, J.M. et al. (2017) The BABY BOOM transcription factor activates the LEC1-ABI3-FUS3-LEC2 network to induce somatic embryogenesis. *Plant Physiology*, 175(2), 848–857. Available from: https://doi.org/10.1104/pp.17.00232

Jarvis-Lowry, B. (2023) Aspects of the biology and control of old man's beard (*Clematis vitalba*). PhD thesis. Massey University, New Zealand.

Jeník, J. (1994) Clonal growth in woody plants: a review. *Folia Geobotanica*, 29(2), 291–306. Available from: https://doi.org/10.1007/BF02803802

Kennedy, P.C. (1982) The general morphology and ecology of *Clematis vitalba*. The *Clematis vitalba* threat: distribution and control of the introduced weed old man's beard (*Clematis vitalba*). *New Zealand Department of Lands and Survey Information Series*, 11, 26–34.

Kevers, C., Hausman, J.-F., Faivre-Rampant, O., Dommes, J. & Gaspar, T. (2009) What we have learned about the physiology of in vitro adventitious rooting of woody plants and how it relates to improvements in the practice. In: Niemi, K. (Ed.) *Adventitious root formation of forest trees and horticultural plants – from genes to applications*. Kerala: Research.

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2017) lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26. Available from: https://doi.org/10.18637/jss.v082.i13

Ladwig, L.M. & Meiners, S.J. (2015) The role of lianas in temperate tree communities. In: Schnitzer, S.A., Bongers, F., Burnham, R.J. & Putz, F.E. (Eds.) *Ecology of lianas*. West Sussex: Wiley Blackwell, pp. 188–202.

Larson, K.C. (2000) Circumnutation behavior of an exotic honeysuckle vine and its native congener: influence on clonal mobility. *American Journal of Botany*, 87(4), 533–538. Available from: https://doi.org/10.2307/2656597

Leicht-Young, S. & Pavlovic, N.B. (2015) Lianas as invasive species in North America. In: Schnitzer, S.A., Bongers, F., Burnham, R.J. & Putz, F. E. (Eds.) *Ecology of lianas*. Chichester, West Sussex: Wiley Blackwell.

Leicht-Young, S.A., Latimer, A.M. & Silander, J.A. (2011) Lianas escape self-thinning: experimental evidence of positive density dependence in temperate lianas *Celastrus orbiculatus* and *C. scandens*. *Perspectives in Plant Ecology, Evolution and Systematics*, 13(3), 163–172. Available from: https://doi.org/10.1016/j.ppees.2011.04.002

Marshall, C. (1990) Source-sink relations of interconnected ramets. In: Groenendael, J. & de Kroon, H. (Eds.) *Clonal growth in plants: regulation and function*. The Hague: SPB Academic Publishing, pp. 23–41.

Mogie, M. & Hutchings, M.J. (1990) Phylogeny, ontogeny and clonal growth in vascular plants. In: Van Groenendael, J. & De Kroon, H. (Eds.) *Clonal growth in plants: regulation and function*. The Hague: SPB Academic Publishing, pp. 23–41.

Mori, H., Masaki, T., Tsunamoto, Y. & Naoe, S. (2020) Survival rate and environmental response of current-year seedlings of the temperate liana *Wisteria floribunda* across a heterogeneous environment. *Journal of Plant Research*, 133(2), 193–203. Available from: https://doi.org/10.1007/s10265-019-01163-1

Mori, H., Ueno, S., Matsumoto, A., Kamijo, T., Tsumura, Y. & Masaki, T. (2018) Large contribution of clonal reproduction to the distribution of deciduous liana species (*Wisteria floribunda*) in an old-growth cool temperate forest: evidence from genetic analysis. *Annals of Botany*, 121(2), 359–365. Available from: https://doi.org/10.1093/aob/mcx153

Munné-Bosch, S. (2015) Senescence: is it universal or not? *Trends in Plant Science*, 20(11), 713–720. Available from: https://doi.org/10.1016/j.tplants.2015.07.009

Oborny, B. & Bartha, S. (1995) Clonality in plant communities – an overview. *Abstracta Botanica*, 19, 115–127.

Ogle, C.C., Cock, G.D.L., Arnold, G. & Mickleson, N. (2000) Impact of an exotic vine *Clematis vitalba* (F. Ranunculaceae) and of control measures on plant biodiversity in indigenous forest, Taihape, New Zealand. *Austral Ecology*, 25(5), 539–551. Available from: https://doi.org/10.1046/j.1442993.2000.01076.x

Ott, J.P., Klimešová, J. & Hartnett, D.C. (2019) The ecology and significance of below-ground bud banks in plants. *Annals of Botany*, 123(7), 1099–1118. Available from: https://doi.org/10.1093/aob/mcz051

Penalosa, J. (1984) Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica*, 16(1), 1–9. Available from: https://doi.org/10.2307/2387886

Peterson, R.A. (2021) Finding optimal normalizing transformations via bestNormalize. *The R Journal*, 13(1), 310–329. Available from: https://doi.org/10.32614/RJ-2021-041

Putz, F.E. (1984) The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, 65(6), 1713–1724. Available from: https://doi.org/10.2307/1937767

R Core Team. (2022) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/ [Accessed 12th December 2022].

Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P. et al. (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Diversity and Distributions*, 13(1), 126–139. Available from: https://doi.org/10.1111/j.1366-9516.2006.00314.x

Roiloa, S.R., Sánchez-Rodríguez, P. & Retuerto, R. (2014) Heterogeneous distribution of soil nutrients increase intraspecific competition in the clonal plant *Glechoma hederacea*. *Plant Ecology*, 215(8), 863–873.

Sakai, A., Nomiya, H. & Suzuki, W. (2002) Horizontal distribution of stolons of a temperate liana *Wisteria floribunda* DC. And its ecological significance. *Journal of Forest Research*, 7(3), 125–130. Available from: https://doi.org/10.1007/BF02762600

Schnitzer, S.A., Dalling, J.W. & Carson, W.P. (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*, 88(4), 655–666. Available from: https://doi.org/10.1046/j.1365-2745.2000.00489.x

Schnitzer, S.A., Parren, M.P.E. & Bongers, F. (2004) Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon. *Forest Ecology and Management*, 190(1), 87–98. Available from: https://doi.org/10.1016/j.foreco.2003.10.008

Schurko, A.M., Neiman, M. & Logsdon, J.M. (2009) Signs of sex: what we know and how we know it. *Trends in Ecology & Evolution*, 24(4), 208–217. Available from: https://doi.org/10.1016/j.tree.2008.11.010

Su, Y.H., Tang, L.P., Zhao, X.Y. & Zhang, X.S. (2021) Plant cell totipotency: insights into cellular reprogramming. *Journal of Integrative Plant Biology*, 63(1), 228–243. Available from: https://doi.org/10.1111/jipb.12972

Tailor, A., Kumari, A., Gogna, M. & Mehta, S. (2022) Chapter 5 – Revisiting the anatomical changes during adventitious root formation in cuttings. In: Husen, A. (Ed.) *Environmental, physiological and chemical controls of adventitious rooting in cuttings*. London: Academic Press, pp. 101–132.

Tichý, L. (2019). GLAMA – gap light analysis mobile application (version 3.0). Czech Republic: Department of Botany and Zoology, MU Brno. Available from: https://play.google.com/store/apps/details?id=new4.glama.glamanew4 [Accessed 26th January 2021].

Van Gardingen, J.R. (1986) The physiological ecology of *Clematis vitalba* L. Master's thesis. University of Canterbury, New Zealand. Available from: https://ir.canterbury.ac.nz/handle/10092/7126 [Accessed 14th March 2020].

Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S*, 4th edition. New York: Springer. Available from: https://www.stats.ox.ac.uk/pub/MASS4/ [Accessed 27th December 2023].

Ward, B.G. & Henzell, R.F. (2000) Herbicide gels for controlling old man's beard (*Clematis vitalba*) in ecologically sensitive areas. *New Zealand Plant Protection*, 53, 284–288.

West, C.J. (1992) *Ecological studies of Clematis vitalba (old man's beard) in New Zealand. Land Resources Vegetation Report 736*. Department of Science and Industrial Research (DSIR): New Zealand.

Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag. Available from: https://ggplot2.tidyverse.org/ [Accessed 23th September 2022].

Wyka, T.P., Zadworny, M., Mucha, J., Żytkowiak, R., Nowak, K. & Oleksyn, J. (2019) Species-specific responses of growth and biomass distribution to trellis availability in three temperate lianas. *Trees*, 33(3), 921–932. Available from: https://doi.org/10.1007/s00468-019-01828-3

Yorke, S.R., Schnitzer, S.A., Mascaro, J., Letcher, S.G. & Carson, W.P. (2013) Increasing liana abundance and basal area in a tropical forest: the contribution of long-distance clonal colonization. *Biotropica*, 45(3), 317–324. Available from: https://doi.org/10.1111/btp.12015

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Jarvis-Lowry, B., Harrington, K.C., Ghanizadeh, H. & Robertson, A.W. (2024) Potential importance of vegetative spread and fragment regeneration for invasiveness of *Clematis vitalba*. *Weed Research*, 1–8. Available from: https://doi.org/10.1111/wre.12633