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REVIEW PAPER

Threats to ecosystems and methods for controlling invasive vines in temperate forests

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ABSTRACT

Climate change, attributable to anthropogenic greenhouse gas emissions, is widely believed to be one of Earth's greatest environmental threats. Forecasts from the literature indicate that the growing greenhouse effect will have a serious impact on the migrations of organisms, causing especial danger to forest ecosystems. Thus, better understanding of the biology of invasive plants, which pose the risk of significantly reduced biodiversity in forest ecosystems, becomes of special importance. Wetlands and river valleys, a significant part of which belong to Natura 2000 habitats, are particularly vulnerable to such invasions. In the case of forests, this situation occurs in riparian and alder carrs, where vines play an important role. This paper presents a review of the research on invasive species of vines that pose a threat to ecosystems in the temperate zone. *Celastrus orbiculatus*, *Clematis vitalba*, *Echinocystis lobata* and *Parthenocissus inserta* are climbers of importance for forestry and forest ecosystems. This paper also discusses current methods of controlling these species when they occur in forest communities. Some strategies these species use to spread and the threats they cause to forest communities are also described; the role of seeds and how they spread have been given special attention. An outline of a research strategy for the invasive species of wild climbing plants, the genomes of which, unlike the *Arabidopsis* model plant, are poorly known, is also presented. In such a situation the most effective approach seems to be to focus on kinetics and biomechanics of shoots and tendrils, the movements of which determine the potential for competition with autochthonic species.

KEY WORDS

Celastrus orbiculatus, *Clematis vitalba*, *Echinocystis lobata*, measures to limit spread, *Parthenocissus inserta*, threats of native forest communities

Introduction

Climate change is one of the greatest environmental threats on Earth in the 21st century, which results primarily from greenhouse gas emissions. Forecasts from the world literature predict that the intensifying greenhouse effect will lead to serious migrations of organisms, causing particular danger to forest ecosystems (Thuiller *et al.*, 2005).Thus, the problem of understanding the biology of growth and development of allochthonous invasive plants, which compete with native species and cause the risk of a significant reduction in biodiversity in forest ecosystems, acquires special importance (Huntley, 1991).

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For thousands of years man has contributed to changes in the natural environment. However, the beginning of these changes is usually considered to be the turn of the 15th to the 16th century, when intense geographical discoveries took place, and the period of great human migrations began. Plants migrated together with humans, settling new continents. Initially, foreign species were considered harmless and were widely introduced to crops. Currently, most woody invasive plants in the United States are believed to have been introduced for horticultural purposes (Reichard and White, 2001). Favourable growing conditions and lack of natural enemies caused these plants to spontaneously occupy new areas and limit the growth of native species (Kołaczkowska, 2008). Nowadays, invasive alien species are one of the main threats to biodiversity (Genovesi, 2005; Tokarska-Guzik *et al.*, 2015).

Kowarik (1995) distinguished two phases of land occupation by alien species. The first consists of the slow colonization of new areas and the subsequent phase of rapid invasion. The length of these phases depends on the life cycle of a given plant. In recent decades, significant environmental changes have been observed around the world. Not only are parameters such as temperature and increasing carbon dioxide emissions being monitored, but increasing attention is also being paid to changes in native flora and fauna (Araujo and Rahbek, 2006). The most important factor in the establishment of alien species in a new site is the prevailing climate. Some of the plants brought to a new area are killed by drought or frost (Bradley *et al.*, 2009). Others, that originate from areas with similar conditions, become established and begin to colonize new areas. It is now thought that plant species may be harbingers of coming climate change due to their high potential to colonize new areas and damage native species (Clements and Ditommaso, 2011). Non-native plants often respond positively to disturbances associated with climate change, and some are more competitive due to increased carbon dioxide (Smith *et al.*, 2000; Ziska *et al.*, 2005; Thuiller *et al.*, 2006). Therefore, in the face of climate change, many invasive plant species will be in the process of developing appropriate adaptations (Davis and Shaw, 2001, Christmas *et al.*, 2016). This could lead to exponential population growth of alien species in the near future. Consequently, when assessing the threat of invasive species, their evolutionary potential must be considered (Clements and Ditommaso, 2011). For this assessment, species distribution models are used which suggest that the proportion of alien species, including invasive species, will increase with climate change. Appropriate management and protection planning are often crucial in conserving areas of special natural value (Vicente *et al.*, 2013). It is believed that alien species can lead to a complete disruption of the network of ecological relationships in an existing ecosystem (Faliński, 2004). The decrease in the number of native species, due to the appearance of alien newcomers, has its consequences in terms of ecology, but also poses a threat to the existing landscape (Hejda *et al.*, 2009).

Different types of wetlands, such as marshes, swamps, floodplain communities, and river valleys are particularly vulnerable to similar invasions. These provide favourable conditions for colonization due to the availability of water, light, and nutrients (DeFerrari and Naiman, 1994). A number of non-native wetland species form monotypes that alter plant community structure, reducing diversity and modifying nutrient cycles (Zedler and Kerche, 2004). This process is amplified near urban areas, where access to alien diaspores is virtually unlimited (Knapp *et al.*, 2010; Dyderski and Jagodziński, 2016). In the case of forest areas, a similar situation also arises in riparian communities, where plants from the vine group are common. This is related to disturbances in coastal zones, where coastal vegetation has been removed as a result of periodic flooding or anthropogenic disturbances. Invasive plants affect ecosystems through changes in the flow of energy and the cycling of matter, changes in habitat characteristics, and the use of available resources (Grašič *et al.*, 2019).

In Europe, the problem of invasive vine species is becoming increasingly important (Drake, 2009). Forecasts from the literature predict that the migration of organisms may pose a threat to forest ecosystems. Therefore, the problem of understanding the biology of growth and development of allochthonous invasive plants, which are competition for native species, is of special importance, causing the risk of a significant reduction in biodiversity in forest ecosystems. Currently, alien vines are found in many countries of Central and South-Eastern Europe, where they pose a threat and where effective methods of their control are sought (Sundarapandian *et al.*, 2015).

Invasive vines in temperate forests

One of the most important roles among invasive vines in forest ecosystems is assigned to the oriental bittersweet *Celastrus orbiculatus* Thunb., which is a naturally occurring vine in East Asia. It was brought to the U.S. in the 18th century as a decorative plant, but after some time it became a weed. Currently, it is an invasive species in the U.S. (Pande *et al.*, 2007) and New Zealand (Williams and Timmins, 2003). So far, this species has not posed a serious threat to European forests, but similar environmental conditions for plant growth in the temperate zone indicate that the risk of its appearance in Central Europe may occur relatively soon. Oriental bittersweet can damage trees by girdling or interfere with forest regeneration by shading smaller native seedlings and young trees. This plant remains in a dim place under the canopy for a very long time, and responds to canopy disturbance with rapid growth, often overtopping trees (Greenberg *et al.*, 2001; Leicht-Young *et al.*, 2009). It grows up to 12 m in height. The diameter of the trunk of this plant is about 5 cm, although specimens with DBH of 14 cm have been found. The flowers are set on short stalks in one or more inflorescences. Fruits are round, 6-8 mm in diameter. The seeds and fruits provide food for birds and mammals which could be the seed dispersal vector (Lafleur *et al.*, 2007). This vine is a threat to native flora and can often be found along roadsides and forest gaps (Dreyer *et al.*, 1987). This species has the ability to modify habitats. The presence of *C. orbiculatus* leads to higher soil pH and potassium, calcium and magnesium levels. It also exhibits a high range of tolerance to habitat fertility levels and light availability (Leicht-Young *et al.*, 2009). The rapid growth of this vine leads to problems in silviculture by arresting natural regeneration and seedling growth (McNab and Meeker, 1987). In addition, oriental bittersweet damages young hardwood stands by stem girdling, increasing the risk of damage, and eventually causing death (Putz, 1991).

In Central Europe, *Echinocystis lobata* (Michx.) Torr. & Gray, also known as wild cucumber, is considered one of the most dangerous invasive vines in forest ecosystems. It is a North American species, shown to be invasive in many countries (Tokarska-Guzik *et al.*, 2015; Ielciu *et al.*, 2017). It appeared in Europe at the turn of the 20th century. It was imported intentionally as a decorative plant and, at the same time, brought in with cotton shipments (Bagiand Böszörményi, 2008). The spontaneous appearance of this plant in Europe was found in the early 20th century. Currently, it is found in many central and southeastern European countries such as Lithuania (Gudzhinskas, 1989), Latvia (Rutkovska *et al.*, 2011), Ukraine (Konishchuk *et al.*, 2020), Russia (Vinogradova *et al.*, 2018), Romania (Ielciu *et al.*, 2017), Hungary (Bagi and Böszörményi, 2008), and Slovenia (Grašič *et al.*, 2019). It came to Poland around 1950, probably from Germany and Ukraine. The first records of this vine in the wild came from areas near Kraków and Lublin (Tokarska-Guzik, 2005). Currently, it is also on the list of Europe's 100 most invasive alien species (Drake, 2009; Vilà *et al.*, 2009). Over the past few decades, this species has significantly increased its area of distribution. Wild cucumber is an annual vine in the *Cucurbitaceae* family (Barber, 1909; Silvertown, 1985). It is a very light-demanding species. It severely limits the availability of light to native species, preventing them from further growth. As it grows it climbs the surrounding herbaceous plants, shrubs, and trees. It is characterized by very rapid growth during the growing season (Klotz, 2009; Adamowski *et al.*, 2014). The stem grows to about 6-8 meters in length. The shoot is sparsely hairy with numerous branching tendrils. The tendrils, located at the angles of the leaves. grow to about 20 cm in length (Gerrath *et al.*, 2008) and 4 of them are gathered at a node. They constitute the primary climbing mechanism of this plant. When in contact with a support or another plant, it hooks onto it with its tendrils, which then take the form of a spring (Bagi and Böszörményi, 2008). Wild cucumber is a monoecious plant. It usually blooms from mid-June to August (Gerrath *et al.*, 2008). The plant reproduces solely by seeds, which mature in the fall and are released irregularly (Klotz, 2009). Most of them fall out of the fruit immediately after opening, the rest only after it dries (Dylewski *et al.*, 2018). Fresh, mature seeds are dormant and must undergo stratification for successful germination (Choate, 1940; Bagi and Böszörményi, 2008; Grašič *et al.*, 2019). The weight of one thousand seeds is between 256.8-293.0 g, the specific gravity is 1.0847-1.0979 g/cm^3 (Bagi and Böszörményi, 2008). Seeds usually germinate near the mother plant (Dylewski *et al.*, 2018). They can also be carried by water currents, which allows for rapid colonization of successive shoreline sections (Dajdok and Kącki, 2009; Klotz, 2009; Adamowski *et al.*, 2014; Grašič *et al.*, 2019). The seed lifespan is more than one year (Klotz, 2009). *E. lobata* prefers riverine woodland and anthropogenic habitats. Despite its wide range of occurrence, the greatest threat to native biodiversity occurs in riverside herbaceous areas and riparian edges (Priede, 2008; Kołaczkowska, 2010, 2012), of which a significant portion is included in Natura 2000 habitats (Kołaczkowska, 2016).

The old man's beard *Clematis vitalba* L. is a vine in the *Ranunculaceae* family, native to Britain, Central and Southern Europe, and the Caucasus (Hill *et al.*, 2001). It is a woody, perennial, deciduous vine and has been introduced as an ornamental plant in gardens worldwide (Redmond and Stout, 2018). This plant produces bright flowers that bloom between July and September (Hill *et al.*, 2001). Stems can grow an average of 2.3 m in 1 year, producing 20 new nodes. The plant spreads by seed and adventitious roots. The average seed-fall is 65 seeds/m^2 in 1 year and the estimated life of seed in the soil is 8-10 years (Gourlay *et al.*, 2000). Its seeds are dispersed by the wind; thus it is possible to spread diasporas from gardens and establish new populations in the wild. It is considered an invasive species in many countries (Hill *et al.*, 2001). It has become a well-known invasive plant threatening the existence of many New Zealand native forest remnants. The old man's beard is responsible for causing structural changes to forest canopies and facilitates the establishment of other invasive plants (Ogle *et al.*, 2000). The vine climbs forest trees, forming a dense canopy, which can reduce healthy forest to a low thicket of vines (Gourlay *et al.*, 2000). The seeds of this species show a high degree of embryo dormancy, which is a common feature of many invasive species occupying new areas. The main factors regulating the awakening of the embryos are light and temperature. Requiring coolness for germination has obvious potential ecological benefits for species growing in seasonal climates, delaying germination until after winter when temperatures are more suitable for seedling growth and survival (Bungard *et al.*, 1997). It seems that the ecological importance of the light requirement for germination is primarily related to the avoidance of too deep germination in the soil, which could be an important mechanism for detecting crown gaps, allowing seeds to grow in a more favourable environment for plants (Grime *et al.*, 1981; Bungard *et al.*, 1997). The plant colonizes forest edges where there is plenty of light, and moves towards the center of the forest as the outer trees fall over. It accesses forests along roads, waterways, and other gaps. It can also be found along riverbanks and in gardens and shelterbelts. The development of seedlings under the canopy of the stand is also observed, which may suggest the dispersal of seeds by animals (Bungard *et al.*, 1997).

The old man's beard prefers the habitats of natural and plantation forests, riverbanks, agricultural areas, coastland, grasslands, riparian zones, disturbed sites, shrublands, and urban areas (Gourlay *et al*., 2000; Sundarapandian *et al*., 2015).

Parthenocissus inserta (A.Kern.) Fritsch, also known as thicket creeper, false Virginia creeper, woodbine, or grape woodbine, is a woody vine native to North America. It was introduced to Europe as an ornamental climber, where it then spread to neighboring areas and is now seen in many European countries (Vegh *et al*., 2015). It occurs mainly in deciduous forests, where it climbs adjacent trees or covers the vegetation of the forest floor. It is also found as a shrub plant in urban areas in less intensively developed places (Zieliński *et al*., 2012). *P. inserta* penetrates natural, semi-natural, and disturbed communities (Kozlovskiy *et al*., 2020). It is a sprawling woody vine, which usually climbs to the height of 15-20 m (Zieliński *et al*., 2012; Kozlovskiy *et al*., 2020). It is characterized by rapid growth of 1-2 m per year (Sołtys-Lelek and Barabasz--Krasny, 2010). In riparian forests the vine creates a vast patch where it dominates, displacing other species from the native plant layer. On the riverbanks, it forms dense thickets to occupy a vacant niche. In the riparian forest, being the only representative of understory vegetation, it climbs along the tree trunks of the first and second stratum. In the lower part, the shoots branch little and lack leaves. In the crowns at illuminated places, they intensely branch, forming a dense leaf mosaic. This vine is a competitor for light with the tallest trees (Kozlovskiy *et al*., 2020). It employs small, branched tendrils with twining tips to latch on to existing supports and other plants. The leaves are compound, with five leaflets. The flowers are small and greenish, produced in clusters in late spring, and mature in late summer or early fall into small blue-black berries (Zieliński *et al*., 2012). *P. inserta* is closely related and often confused with *P. quinquefolia* (L.) Planch (Virginia creeper). They differ in the way of climbing and the construction of the tendrils. *P. inserta*, unlike *P. quinquefolia*, lacks tendrils, terminating in an adhesive disc. Consequently, it only climbs bushes and trees, avoiding smooth surfaces (Gerrath and Posluszny, 1989; Kozlovskiy *et al*., 2020). *P. inserta* is a very temperature-resistant species – it tolerates temperatures to –30°C. It is also drought tolerant. It grows well and develops without watering, tolerates drought without damaging the aboveground organs. Reversible wilting of some leaves is observed. Buds and seeds develop normally the following year after the drought. Self-seeding is recorded only in damp, shaded places (floodplains, ravines, and gullies, ditches, shrubbery). *P. inserta* seeds collected in the oak forest have the following characteristics: the weight of 1000 seeds was 28.1 ±1.1 g, laboratory germination 62%. Studies have shown that the duration of cold stratification (temperature 0-5°C) for seed germination should be at least 75 days, although seeds stored for 100 days are most effective. (Kozlovskiy *et al*., 2020). The species reproduces by seeds and rooting shoots. The dispersion of seeds occurs with the participation of wind (anemochory), with water (hydrochory), spontaneously (autochory), or with the participation of animals (zoochory) (Sołtys-Lelek and Barabasz-Krasny, 2010; Kozlovskiy *et al*. 2020). However, in the presence of other fruits, *P. inserta* berries are not readily eaten by birds. Most of the berries fall off the crowns of trees during the winter, forming temporary seed banks from which new plants germinate in the spring (Tomson and Grime, 1979; Kozlovskiy *et al*., 2020).

Measures to limit spread in forests

Oriental bittersweet is highly competitive with native vegetation and potentially difficult to manage in forests; therefore, various control methods are being examined (McNab and Loftis, 2002). Biological enemies of this plant include sac fungi: *Microsphaera celastri* Y.N. Yu & Y.Q. Lai, *Uncinula sengokui* Salm., *Amazonia celastri* Y.X.Hu & B.Song) and insects: *Hypothenemus eruditus*

Table 1.

List of invasive vine species with details on their nativity, continents invaded, habitat ecology, impacts on ecosystems. and control measures, in various studies

Species	Family	Native continent	Continent(s)/ area invaded	Habitat	Impacts on ecosystem	Control measures	Sources
Celastrus orbiculatus Thunb.	*Celastraceae*	Asia	North America, Oceania	Agricultural areas, coastland, northern hardwood forest, grasslands, riparian zones, disturbed sites, shrublands, urban areas	Seeds have a high ability to germinate under a variety of light conditions, affects higher soil pH and potassium,calcium, and magnesium levels, exhibits a high range of tolerance to habitat fertility levels and light availability	Mechanical, chemical, and biological	Sundarapandian *et al.*, 2015; Dreyer *et al.*, 1987 Leicht-Young *et al.*, 2009
Echinocystis lobata (Michx.) Torr. & Gray	*Cucurbita-ceae*	North America	Europe	Rush, scrub, riverine woodland habitats, anthropogenic habitats, riverside herbaceous areas, mountain herb fringes, riparian herb fringes, looded silty river banks and riparian forests	Limits the availability of light to native species preventing them from further growth	Mechanical, chemical, and biological methods to a very limited extent	Priede, 2008; Kołaczkowska, 2010, 2012, 2016; Silvertown, 1985; Protopopova *et al.*, 2015
Clematis vitalba L.	*Ranuncu-laceae*	Asia, Europe	Oceania, North America	Agricultural areas, coastland, forests, grasslands, riparian sites, disturbed sites, shrublands, urban areas	Limits the availability of light for the tallest trees, forming a dense, light absorbing canopy that suppresses all vegetation beneath it and causes breakage of branches	Mechanical, chemical, and biological	Gourlay *et al.*, 2000; Sundarapandian *et al.*, 2015; Redmond and Stout, 2018
Parthenocissus inserta (A.Kern.) Fritsch	*Vitaceae*	North America	Europe	Anthropogenic habitats, urban areas, ruderal habitats, riverside areas, forest edge, riparian forests, peat bogs, urban forests, parks, gardens, public squares, in the courtyards of high-rise and private residential developments, country cottage partnerships, cemeteries	Causes deformation of trees and shrubs, limits the availability of light for seedlings and undergrowth species, has allelopathic properties, deforms plant communities		Wika and Gorczyca, 2006; Kozlovskiy *et al.*, 2020

Westw., *Plinachtus bicoloripes* Scott, *Unaspis euonymi* (Comstock), *Trioza celastrae* Li, *Yponomeuta sociatus* Moriuti (Lynch, 2009). Methods of controlling this vine include mechanical and chemical treatments. Young populations are controlled treated by cutting and applying triclopyr herbicide to the regrowth about a month later. Larger vines can be pruned, and the stump treated with the herbicide triclopyr (Dreyer, 1994; Mervosh and Gumbart, 2015).

Due to the high risk of *E. lobata* in Poland, there are treatments aimed at limiting its occurrence, primarily in forest areas, especially those under protection. Control treatments include mechanical and chemical methods. Mechanical methods involve pulling and mowing plants before they produce seeds. The best results are obtained by pulling out young seedlings in the spring. During this period they are easy to locate and remove. These treatments should be repeated annually, and the removed plants burned outside protected areas to reduce the risk of further spread. Chemical methods involve applying substances containing glyphosate to the plant, preferably in early spring (Kołaczkowska, 2016). However, the use of chemical methods, especially in forested areas and near water, is highly controversial and prohibited in many European countries (Starfinger *et al.*, 2003). In the U.S., natural enemies of the plant such as the beetle *Acalymma vittata* (F.) (Coleoptera: *Chrysomelidae*) have been reported to limit its spread (Silvertown, 1985). In Europe, no insect species have yet been known to be effective as a biological method for the control and reduction of *E. lobata* (Buszko, 2015). However, it has been noted that rodents and birds may be involved in the reduction of seeds that are their potential food, but on the other hand, contributing to their dispersal by carrying and collecting them (Dylewski *et al.*, 2019).

Old man's beard *C. vitalba* has an adverse effect in lowland forests that can be attributed to the high biomass accumulation of the vine in the treetops. Controlling the impact of such an expansive plant using classical biological control is difficult because of the plant's ability to produce so many wind-born seeds. Known effective biological control agents include *Phytomyza vitalbae* Kaltenbach. Studies have shown that development of a *P. vitalbae* population can effectively limit the growth of old man's beard. Flies are abundant in early spring when plant growth is fastest and can therefore have a greater effect on plant growth (Gourlay *et al.*, 2000; Hill *et al.*, 2001; Paynter *et al.*, 2008). Other potential species, such as *Xylocleptes bispinus* (Duftschm.) and *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc., have been effective in reducing the occurrence of old man's beard, but since it is not the sole host, they may have negative effects on other *Clematis* spp. (Gourlay *et al.*, 2000). Mechanical methods consist of cutting the vine shoot at a height from the ground of 1 m and then painting the stumps with a combination of 2,4,5-T and Multi-film penetrant (Smith, 1984). Old man's beard regrowth should be controlled by hand and/or by spot-spraying by substances containing 1% glyphosate (Ogle *et al.*, 2001).

Parthenocissus inserta is a competitor for native vegetation and hinders its development by entangling with meandering shoots and shading the forest floor. Elimination of *P. inserta* should be done mechanically by mowing and uprooting, especially of young specimens. Due to frequent coexistence with other species, chemical methods are not recommended. The cultivation of *P. inserta* should be avoided in the vicinity of commercial and natural forests, protected areas and their surroundings, and watercourses. It is recommended that acoustic screens, openwork structures, and buildings should not be planted with this vine (Stalmachová *et al.*, 2019). The mechanical method involves cutting the shoots just above the ground surface (e.g., with a brush cutter), and then removing the drying mass from the supports (*e.g.*, trees and shrubs) and the ground surface. Then all rooted parts of the species should be pulled out along with any new individuals that appear in order to prevent the seed bank from remaining in the soil. This species should be controlled for at least 3-4 seasons. Another measure to limit the spread of the plant is the removal of seedlings and weeding of the regrown plants by hand (Krzysztofiak *et al.*, 2018).

Discussion

Over the past few decades, ecologists have been interested in how invasive plants affect ecosystems. Negative interactions between non-native and native species in forests are an important topic in ecosystem research (Mack *et al.*, 2000). It is believed that mature and old forests do not contain numerous invasive vines, because their development is limited by the low level of light reaching the forest floor (Brothers and Spingarn, 1992). In studies by Pavlovic and Leicht-Young

Table 2.
List of invasive vines species with a description of the different methods of controlling them in various studies

Species	Mechanical method	Chemical method	Biological method
Celastrus orbiculatus Thunb.	cutting down plants (Dreyer, 1994)	applying triclopyr herbicide (Dreyer, 1994; Mervosh and Gumbart, 2015)	sac fungi (Lynch, 2009): – *Microsphaera celastri*, – *Uncinula sengokui* – *Amazonia celastri* insects (Lynch, 2009): – *Hypothenenmus eruditus*, – *Plinachtus bicoloripes* – *Unaspis euonymi* – *Trioza celastrae* – *Yponomeuta sociatus* birds (Lafleur *et al.*, 2007): – *Sturnus vulgaris* – *Turdus migratorius*
Echinocystis lobata ((Michx.) Torr. & Gray)	pulling and mowing plants before they produce seeds pulling out young seedlings (Kołaczkowska, 2016)	applying glyphosate herbicide (Kołaczkowska, 2016)	insects (Silvertown, 1985): – *Acalymma vittata* mammals (Dylewski *et al.*, 2019): – rodents virus (Rist and Lorbeer, 1989) – *Cucumber Mosaic Virus*
Clematis vitalba L.	cutting the vine shoot at a height between the ground level and 1 m (Smith, 1984) pulling out young seedlings by hands (Ogle *et al.*, 2001)	spraying or painting the stumps with a combination of 2,4,5-T and Multi-film penetrant (Smith, 1984) spot-spraying by substances containing 1% glyphosate (Ogle *et al.*, 2001)	insects (Gourlay *et al.*, 2000): – *Phytomyza vitalbae* – *Monophadnus spinolae* – *Xylocleptes bispinus* – *Thyris fenestrella* – *Horisme vitalbata* – *Melanthia procellata* fungi (Gourlay *et al.*, 2000): – *Phoma clematidina* – *Colletotrichum gloeosporioides*
Partheno-cissus inserta (A.Kern.) Fritsch	mowing and uprooting, especially of young specimens (Stalmachová *et al.*, 2019) cutting the shoots just above the ground surface (Krzysztofiak *et al.*, 2018)	not recommended (Stalmachová *et al.*, 2019)	no data

(2011) on the vines of the southern region of Lake Michigan in mature and old forests, *Celastrus orbiculatus* was present in 30% of the research areas. This species was observed on tree trunks and in a few cases reached the canopy. It was mainly a component of the ground layer. *C. orbiculatus* is considered a serious threat to mature forests as it will persist in the ground layer until a canopy gap or other disturbance provides light. It will then rise to the canopy level and damage mature trees in the stand. As a result, forests in which this vine is present should be monitored by land managers so that the vine can be effectively controlled in times of low density and limited range.

The old man's beard *C. vitalba* is one of the most problematic invasive species in New Zealand's forests. Many ecological and governmental communities are looking for effective ways to control this vine using mainly mechanical and chemical methods (Ogle *et al.*, 2001). In the studies of Bungard *et al.* (2012), no old man's beard was observed in the preserved fragments of the natural forest. On the other hand, this creeper appeared in disturbed parts, most often in gaps in the stand, where the light level exceeded 5%. Many species of invasive vines use the gaps in the stand to grow and, consequently, expand their range and drown out the existing vegetation.

Riparian zones of forest vegetation play an important role in the structure and functions of aquatic ecosystems as the most fertile and productive parts of the landscape (Naiman *et al.*, 1993). Disturbances to riparian zones increase their vulnerability to invasion by alien plant species, through transport of propagules by water currents (Richardson *et al.*, 2007). The wild cucumber *E. lobata* has significantly increased its range in recent years, as a result of the transmission of seeds by water currents. In studies by Dyderski and Jagodziński (2016), over a period of 30 years wild cucumber appeared on more than 80% of the studied areas, in places where it had not been recorded before. In studies by Kopeć *et al.* (2014) on the response of floodplain vegetation to hydroengineering and climatic pressure, an increase in wild cucumber in the alder carrs *Ribeso nigri-Alnetum* was demonstrated; the species was maintained in the disturbed vegetation of riparian forest *Poo trivialis-Alnetum*. In research by Borisova (2011) on invasive species of the Upper Volga River, it was found that wild cucumber is one of the most aggressive plants and plays the role of a transformer. It has established itself in various natural ecotypes and is abundant in damaged habitats. This species shows a wide spectrum of adaptive responses, high ecological plasticity, high seed productivity, and stability to adverse environmental factors. Research by Protopopova *et al.* (2015) has shown that wild cucumber belongs to the group of transformer plants and changes plant phytocoenoses, floristic composition, and structure of such communities as river-bank willow thickets, alder forests, and floodplain meadows, suppressing the aboriginal species and preventing initial plant communities from recovery.

Parthenocissus inserta is present in natural and semi-natural habitats, especially the outskirts of populated areas, abandoned parks, and old plantings (Panasenko and Anishchenko, 2018). Research by Kozlovskiy *et al.* (2020) showed that this species of vines is a sub-edificator in riparian forests in the herbaceous layer. It is the dominant element and creates a stable plant community. It is often the only component of the undergrowth layer from where it grows into other trees with which it competes for light. This species changes the nature of forest biocoenoses over large areas. According to research by Panasenko and Anishchenko (2018), an indicator of a successful invasion by this vine in forest communities is the formation of syn-taxonomically valid plant variants of *Corylo avellanae-Pinetum sylvestris*.

The seeds of many invasive species require periodic cooling. For example, seeds of old man's beard germinate best with periodic cooling and more than 5% light availability (Bungard *et al.*, 2012), and the seeds of wild cucumber need at least 3-6 weeks to germinate effectively (Bagi and Böszörményi, 2008). Likewise, *P. inserta* only sprouts after 75 days of coolness (Kozlovskiy *et al.*, 2020). The dormancy of the embryos is of great evolutionary importance, especially if it concerns species from a temperate climate, where there is seasonality. This allows these seeds to overwinter through an unfavorable period, then germinate in optimal conditions, ahead of native species. Another feature of the seeds of invasive species is the long viability of the seeds, 8-10 years for old man's beard (Gourlay *et al.*, 2000), and more than one year for wild cucumber (Klotz, 2009). A high level of wild cucumber seed production, where one plant is able to produce 40-160 seeds, and a high germination capacity of about 70% favours the spread of the species and its rapid growth, which, together with the simple provision of conditions necessary for growth, leads to the displacement of other species (Protopopova *et al.*, 2015). This allows it to survive unfavourable periods of drought or cold and to germinate in the next growing season.

There is a lot of research into methods of controlling invasive vine species. Most of the research has been focused on mechanical methods, which are mainly limited to cutting whole plants or uprooting young seedlings (Smith, 1984; Dreyer, 1994; Ogle *et al.*, 2001; Kołaczkowska, 2016; Krzysztofiak *et al.*, 2018; Stalmachová *et al.*, 2019). However, these methods are not very effective and to a large extent limited, seeing that these invasive climbing plants persist in forest ecosystems. Many of these vines are associated with aquatic and naturally valuable habitats, where the possibility of using chemical methods is significantly limited (Starfinger *et al.*, 2003). The current known biological methods are not always applicable, and it is necessary to conduct a detailed examination of the organisms intended to fight a given species in terms of potential damage to the natural environment (Lynch, 2009). Uncontrolled expansion of invasive species, especially in areas with strong anthropogenic pressure, may result in unfavourable natural succession and, consequently, destabilization of the ecological system in a given area (Fortuna-Antoszkiewicz *et al.*, 2008). Many invasive vines pose a threat to native plant species. Therefore, it is essential to develop effective control methods to limit the expansion of these species. In recent decades, in the literature on plant biology, attention has been directed mainly to molecular and biochemical studies, conducted primarily on taxa with a fairly well-studied genome, *i.e.*, numerous mutants of the model plant *Arabidopsis*, as well as various varieties of cultivated plant species of fundamental importance for agriculture. In the case of work on wild climbing species, with the character of invasive plants, whose genome is usually very poorly understood, it seems more expedient to apply a different strategy. In this situation, it seems most effective to focus on problems related to kinetics and biomechanics, shoots and tendrils, whose movements determine the possibility of competition with indigenous species (unpublished data of the Department of Forest Botany of the Warsaw University of Life Science – SGGW). They provide an opportunity for a detailed study of the mechanisms of growth of these vines and analysis of the geometry of its movements, which in the future may be used to develop effective methods of control, especially when vines invade areas of particular natural value.

Authors' contributions

A.D.-L. – the research concept, manuscript preparation, manuscript corrections; U.Z. – manuscript corrections, supervision. All authors have read and agreed to the published version of the manuscript.

Conflicts of interest

The authors declare no conflict of interest.

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STRESZCZENIE

Zagrożenia dla ekosystemów i metody zwalczania inwazyjnych pnączy w lasach klimatu umiarkowanego

Od wielu setek lat człowiek przyczynia się do zmian w środowisku przyrodniczym. Uznaje się jednak, że to ostatnie dziesięciolecia jego działalności najbardziej wpłynęły na obecny kształt flory na Ziemi. Przełom XV i XVI wieku to czas intensywnych odkryć geograficznych oraz migracji ludności. Wraz z człowiekiem migrowały również rośliny, zasiedlając nowe kontynenty. Dobre warunki wzrostu i brak naturalnych wrogów sprawiły, że rośliny te spontanicznie zajmowały nowe tereny, ograniczając przy tym rozwój rodzimych gatunków. Znane z literatury światowej prognozy przewidują, że nasilający się efekt cieplarniany skutkować będzie poważnymi migracjami organizmów, powodując szczególne niebezpieczeństwo dla ekosystemów leśnych. Uważa się, że najważniejszym czynnikiem dla zadomowienia się obcych gatunków w nowym miejscu jest panujący tam klimat. Część przywleczonych na nowy teren roślin ginie na skutek panujących w tym miejscu susz lub mrozów. Inne, pochodzące z terenów o podobnych warunkach, zadomowią się i zaczną zajmować nowe terytoria. Uważa się, że obce gatunki roślin mogą być zwiastunami nadchodzących zmian klimatycznych, ze względu na ich duży potencjał zasiedlania nowych terenów oraz powodowania szkód wśród gatunków rodzimych. Rośliny obcego pochodzenia pozytywnie reagują na zaburzenia związane ze zmianą klimatu, a niektóre są bardziej konkurencyjne z powodu zwiększonej ilości dwutlenku węgla. W związku z tym, w obliczu zmian klimatycznych, wiele inwazyjnych gatunków roślin będzie w trakcie tworzenia odpowiednich adaptacji. Może to prowadzić do wykładniczego wzrostu populacji obcych gatunków w najbliższej przyszłości. Ocena zagrożenia inwazyjnych gatunków musi więc uwzględniać ich potencjał ewolucyjny. W tym aspekcie specjalnego znaczenia nabiera problematyka poznania biologii wzrostu i rozwoju allochtonicznych roślin inwazyjnych, stanowiących konkurencję dla gatunków rodzimych i stwarzających ryzyko istotnego obniżenia różnorodności biologicznej w ekosystemach leśnych. Szczególnie narażone na tego typu inwazje są szuwary, tereny podmokłe i doliny rzeczne, których znaczna część należy do siedlisk Natura 2000. W przypadku obszarów leśnych taka sytuacja występuje w zbiorowiskach łęgowych i olszowych, gdzie istotną rolę odgrywają rośliny z grupy pnączy. Do tej pory biologia inwazyjnych gatunków pnączy nie była przedmiotem zbyt intensywnych badań w Europie, a literatura w tej dziedzinie zwykle odnosi się do badań prowadzonych na innych kontynentach. W artykule przedstawiono przegląd badań nad inwazyjnymi gatunkami pnączy, które stanowią zagrożenie dla ekosystemów na innych kontynentach (Ameryka Północna, Oceania i Europa). *Celastrus orbiculatus*, *Clematis vitalba*, *Echinocystis lobata* i *Parthenocissus inserta* są pnączami ważnymi dla leśnictwa i ekosystemów leśnych (tab. 1). W ciągu kilku ostatnich dekad ekolodzy interesowali się tym, jak obce inwazje wpływają na ekosystemy. Negatywne interakcje między gatunkami nierodzimymi i rodzimymi w lasach są ważnym tematem w badaniach ekosystemów. Uważa się, że w dojrzałych i starych lasach nie ma licznych inwazyjnych pnączy, gdyż ich rozwój jest ograniczony przez niski poziom natężenia światła docierającego do dna lasu. Badania nad pnączami wykazują ich przewagę nad rodzimymi gatunkami ze względu na wiele adaptacji, takich jak długa żywotność nasion oraz wysoki zakres tolerancji na wiele czynników, co pozwala im wygrywać konkurencję o zasoby. W pracy omówiono również stosowane obecnie metody zwalczania tych gatunków w przypadkach, gdy występują one na siedliskach szczególnie cennych przyrodniczo oraz w zbiorowiskach leśnych (tab. 2).

Istnieje wiele badań dotyczących metod zwalczania inwazyjnych gatunków z grupy pnączy. Większość z nich skupia się na metodach mechanicznych, które ograniczają się głównie do cięcia całych roślin lub wyrywania młodych. Metody te są jednak mało skuteczne i w dużym stopniu ograniczone, ze względu na szybką kolonizację nowych przylegających terenów oraz wykorzystywanie prądów wodnych do kolonizacji linii brzegowej. Wiele z tych roślin jest związanych z siedliskami wodnymi i cennymi przyrodniczo, gdzie możliwości stosowania metod chemicznych są znacznie ograniczone. Dotychczas znane metody biologiczne nie zawsze mają zastosowanie i konieczne jest przeprowadzenie szczegółowych badań organizmów przeznaczonych do walki z danym gatunkiem pod kątem potencjalnych szkód w środowisku naturalnym. Opisano również niektóre strategie rozprzestrzeniania się tych gatunków oraz zagrożenia, jakie stanowią dla drzewostanów. Zwrócono szczególną uwagę na rolę nasion i sposoby ich rozprzestrzeniania. Przedstawiono również zarys strategii badawczej nad inwazyjnymi gatunkami dzikich roślin pnących, których genom, w przeciwieństwie do rośliny modelowej *Arabidopsis*, jest bardzo mało poznany. Zwrócono uwagę, że w takiej sytuacji najskuteczniejsze wydaje się skoncentrowanie się na zagadnieniach związanych z kinetyką i biomechaniką pędów i wąsów, których ruchy decydują o potencjale konkurowania z gatunkami autochtonicznymi.