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# A resource capture efficiency index to compare differences in early growth of four tree species in northern England.

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## Key words:

Eucalyptus gunnii, Fraxinus excelsior, Acer pseudoplatanus, Alnus glutinosa, resource capture efficiency

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## Abstract

At a trial established in Cumbria, northern England, significant differences in growth rate between tree species were apparent, with cider gum (*Eucalyptus gunnii*) and alder (*Alnus glutinosa*) exhibiting most rapid volume and biomass accumulation. Estimations were made of leaf area, specific leaf area, leaf area ratio (based on stem mass not whole tree mass) and length of growing season. These measurements were undertaken to explain tree growth difference and developing a growth potential index based on growing season length and leaf area. The high leaf area of cider gum and alder explained some of their superior growth, while alder also had the longest period in leaf, compared with ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus*). The slow growth of ash can be explained by the short period in leaf and also the relatively low leaf area ratio.

Leaf area to stem weight also differed between species with that of ash being relatively low. Specific leaf area was also low for ash, a trait shared with cider gum, which suggests that these species invest highly in each unit of leaf area. Of the tree species assessed, the length of the growing season was longest for alder, enabling it to maintain growth for a longer period. By multiplying growing season by leaf area a resource capture index was calculated and this explained 56% of the variation in stem dry weight between trees. The potential and limitations for using this index are discussed.

## Introduction

This paper compares the early growth at a trial in northern England of four broadleaved trees species identified as having potential for short rotation forestry (Hardcastle 2006). Short rotation forestry for bioenergy was identified as a cost-effective and rapid means of reducing greenhouse gases in Matthews and Broadmeadow (2009), yet there is very limited experience of such systems in the UK. While quantifying yields from tree species in short rotation forestry systems is crucial, understanding the underlying factors contributing to their productivity is also important. Yield varies considerably between tree species and on a specific site is dependent on their resource capture efficiency and resource use efficiency (Stape et al. 2004). Resource capture efficiency represents how efficiently a tree is able to allocate its resources to harvesting light for photosynthesis. There are two components; leaf mass fraction (LMF) and specific leaf area (SLA) (Poorter et al. 2012). LMF (the ratio of leaf dry mass to total plant dry mass) reflects the priority of allocation of photosynthate to the leaves. Differences in LMF exist among tree species, with higher LMF being an attribute of faster

53 growing trees (Poorter et al. 2012) and also shade bearing trees (Valladares & Niinemets 2008). LMF  
54 is higher in evergreen than deciduous trees but this is partly because evergreen trees retain leaves  
55 for two or more years (Poorter et al. 2012). This higher LMF in evergreens may therefore be largely  
56 because of the lifespan of the leaf rather than higher partitioning of annual photosynthate to leaves  
57 (Poorter et al. 2012).

58  
59 SLA reflects the amount of resources allocated to each unit of leaf area and is the ratio of leaf area to  
60 leaf dry mass. SLA is generally higher in conifers, compared with broadleaves and higher in fast  
61 growing trees than those that are slow growing. A meta-analysis undertaken by Poorter et al. (2009  
62 in Poorter et al. 2012) found differences in SLA between types of trees were greater than for LMF.  
63 High SLA is a characteristic of plants that have a high relative growth rate (RGR), small seed mass  
64 and both RGR and SLA were good predictors of a plant's potential invasiveness. Leaf area ratio  
65 (LAR) is a variable that combines LMF and SLA, being the ratio between leaf area and total tree  
66 weight and strongly influences RGR, particularly on nutrient rich sites (Poorter & Remkes 1990).

67  
68 Growth of a tree is also influenced by the duration of its growing season. The length of growing  
69 season has a strong influence on a tree's productivity and differences exist among species, origins  
70 and individual trees in terms of their period of dormancy. The dormancy in pioneer trees is largely  
71 determined by temperature, rather than photoperiod. In contrast, late successional trees follow a  
72 more conservative approach, requiring a longer period of chilling and are highly sensitive to  
73 photoperiod (Basler & Korner 2012). Nutrition has also an influence on period of dormancy; tree  
74 species with enhanced access to nutrients, including nitrogen fixing trees like alder adopt a higher  
75 risk approach to the development of their foliage, in a similar way to pioneer trees (Tateno 2003).

76  
77 At this trial, growth was measured but also attributes important in influencing this growth were  
78 quantified, and these were compared between the tree species. A resource capture efficiency index  
79 was devised (leaf area x period in leaf) and its relationship to stem volume was investigated. Results  
80 are compared with those of other researchers and differences observed between the tree species  
81 explained by their ecology.

82  
83 The hypotheses tested were that:

- 84
- 85 • there were differences in volume and biomass growth, SLA and LAR between the tree
- 86 species at the trial;
- 87 • growth of stem volume was positively related to leaf area and growing season;
- 88 • the differences in growth between individuals and species can be explained by their resource
- 89 capture efficiency and other aspects of their ecology.
- 90

## 91 **Materials and methods**

### 92 **The Experiment**

93  
94 A one hectare trial was established at Newton Rigg, Cumbria, England (55°40'56"N, 2°47'22"W) at an  
95 elevation of 160 m above sea level. Ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*) and  
96 alder (*Alnus glutinosa*) were planted in winter 2008 and cedar gum (*Eucalyptus gunnii*) and shining  
97 gum (*Eucalyptus nitens*) in April 2009. Excluding the eucalypts, species selected for the trial were all  
98 classified by EMIS (Perks, Harrison & Bathgate 2006) as being "suitable", rather than "very suitable"  
99 or "unsuitable" for the site. The transplants were cell grown 20-40 cm plants raised by Alba Trees in  
100 the Scottish borders and origins are described in Table 1, along with recommended origins for the  
101 species.

102  
103  
104 <Table 1 here>

105

106 Aspects of the climate at the trial were obtained from the weather station at the Newton Rigg campus  
107 and from The Establishment Management Information System (EMIS) (Perks et al. 2006) and are  
108 shown in Table 2.

109  
110 <Table 2 here>  
111

112 The trial site was originally grass pasture, the soil being a slightly acid (pH6) clay loam brown earth.  
113 Soil bulk density was 0.76 at 0 cm to 15 cm depth and 1.07 at 15 cm to 30 cm depth, while the soil  
114 nitrogen concentration was 0.36g cm<sup>-3</sup> and 0.29 g cm<sup>-3</sup> at 0 cm to 15 cm and 15 cm to 30 cm depth  
115 respectively (Centre for Ecology & Hydrology 2013). Soil depth was not measured but was  
116 sufficiently deep to not be a limitation to early tree growth.  
117

118 The site use was previously improved pasture, which was sprayed before planting with Propazymide  
119 (3.75 litres ha<sup>-1</sup>) to kill the sward. The transplants were planted manually using a “T” notch and  
120 protected in 60 cm tubes. Planting was at 2.5m spacing between rows and 1.5 m spacing within  
121 rows giving a stocking rate of 2,667 stems ha<sup>-1</sup>. Routine spraying of weeds was undertaken twice  
122 during each growing season using glyphosate (5 litres ha<sup>-1</sup>). The design adopted for the trial was a  
123 randomised complete block design, which is the most commonly used design in forest experiments  
124 (Wright and Andrew 1976) and large 10 x 8 tree plots were adopted.  
125  
126

## 127 **Measurements and overview of analysis for each study**

128  
129 Measurements taken in the studies are described in the four sections below. For the measurements  
130 two trees of each of the four species were selected randomly from each of the six replicates in the  
131 trial. Shining gum was killed in its first winter and is not included as part of this study.  
132

### 133 **Stem volume and biomass**

134  
135 Height and root collar diameter were measured for the twelve trees of each species in November  
136 2010 (after two growing seasons) and November 2011 (after three growing seasons). Between  
137 November 2010 and 2011 all the cider gum had died and so the later measurements were not  
138 possible for this species. Height was measured using a height rod, while the root collar diameter  
139 was measured to the nearest 0.1 mm using a digital vernier gauge and taking the mean of two  
140 measurements taken at 90° to one another. Stem volumes were calculated using height (h) and  
141 diameter (d) and assuming that the tree stems were conical in shape. To enable stem weights for the  
142 trees to be estimated, wood samples were taken from a different sample of five trees of each species  
143 and sections were cut from the base, middle and top of their stems. Volumes of these stem samples  
144 were measured using a water displacement method using OHAUS analytical standard scales to  
145 measure weight which was converted to a volume using a water density of 1 g cm<sup>-3</sup>. Stem samples  
146 were oven dried at a temperature of 80°C for 3 days, until no further loss in weight was observed and  
147 then weighed again to obtain dry weight. Specific gravity (SG) was then calculated for the wood  
148 samples and SG (g cm<sup>-3</sup>) and V (cm<sup>3</sup>) were multiplied together to estimate whole-stem dry weight of  
149 the study trees.  
150

### 151 **Leaf Area**

152  
153 In September 2010 after two growing seasons, the crowns of the twelve alder, ash and sycamore  
154 trees measured for stem volume were wrapped in plastic bird netting to trap leaves as they fell. For  
155 sycamore the collections of leaves in late October was straightforward as most of the leaves had  
156 already been shed but for alder, many leaves had to be carefully removed from the crowns of the  
157 sample trees. For trees with less than fifty leaves all leaves were measured and for those with more  
158 than 50 leaves, all leaves were counted and a systematic sample of 50 was taken. For each leaf,  
159 length (L) along the mid rib and width (W) at the widest point of the lamina and petiole length (P) was

160 measured to the nearest millimetre. The use of netting to capture leaves proved to be unsuitable for  
161 trapping leaves of ash as their compound leaves disintegrated and some of the small leaflets fell out  
162 of the bird netting. As such, the leaf length and width could not be measured but the leaf stalk (S)  
163 without the leaflets, which remained trapped in the netting was measured for each leaf. For cider  
164 gum, the evergreen species, the method of trapping fallen autumn leaves was not appropriate. For  
165 each of the twelve trees, all the leaves were counted, classified as mature or juvenile and 50 leaves  
166 were removed from the trees in a systematic way from the bottom to top of the trees to ensure a  
167 good spread. Measurements of L, W and P were taken for each type of leaf.  
168

169 From the leaves collected, a sample of forty was taken for each tree species across the range of  
170 sizes. L, W and P was measured and also S for ash and the leaf area (LA) was then determined  
171 using Compu Eye software and an Epson Perfection 1240 flatbed scanner. For cider gum forty  
172 juvenile leaves and forty mature leaves were measured. For all species, leaves were then dried for  
173 48 hours at a temperature of 70°C and weighed to obtain an oven-dried weight (M) using OHAUS  
174 analytical standard scales and following the approach adopted by Verwijst and Wen (1996). As the  
175 original ash leaves had disintegrated new ash leaves were collected at the end of the summer of the  
176 following year for leaf area and weight determination purposes.  
177

178 The total leaf area for the twelve sample trees of the four species was calculated using allometric  
179 methods, similar to the approach adopted in other studies (Wargo, 1978; Verwijst & Wen 1996,  
180 Ugeese et al. 2008, Serdar & Demirsoy 2006). This involved the determination of relationships  
181 between measurements of L and W (and S for ash) to leaf area and leaf weight using least squares  
182 regression. Best fit functions were selected based on  $R^2$  and standard error statistics. Best fit  
183 relationships were used to estimate the leaf area of each leaf sampled from the twelve trees of each  
184 species. For each tree, a mean leaf area was calculated and this was multiplied by the total number  
185 of leaves present to obtain an estimate of total leaf area per tree. For the twelve trees of each  
186 species, the results from the leaf area measurements and of the stem weights were used to SLA (leaf  
187 area/ leaf dry mass) and LAR (leaf area/stem dry weight) parameters. LAR was calculated based on  
188 stem dry weight rather than the whole tree weight as below ground biomass was not assessed.

## 189 **Growing season**

190  
191 The same twelve trees of each species used in the leaf area study, were assessed during 2011 to  
192 determine the length of the third growing season of the tree species at the trial. The method adopted  
193 elements from a study of leaf development in rowan (*Sorbus aucuparia*) (Forest Research no date)  
194 and one investigating leaf senescence in birch (*Betula pendula*) (Worrell 2006). The development  
195 of the bud was scored on a 0-5 scale with 0 for a dormant bud and 5 for full leaf expansion (the scale  
196 was 1 to 6 in original study from Forest Research, no date). The stages in the bud burst scoring  
197 were as follows:  
198

- 199 0. Bud is closed and in a fully dormant winter state
- 200 1. Bud is swollen and the bud scales just started to open, however the bud is still vertical
- 201 2. Bud scales have separated and the tightly furled leaves are visible. The bud is bent sideways and  
202 can appear "hooded"
- 203 3. Bud scales are completely separated, leaves are starting to unfurl and separate but the leaflets  
204 (pinnae) on each leaf remain still furled. The leaves appear brownish in colour since the  
205 underside is predominantly visible.
- 206 4. The leaves are elongated and leaflets have started to separate as well. The appearance is now  
207 much more green since the topside of the leaves is now visible
- 208 5. All leaflets have separated on the lowest two leaves and the shoot is expanding.

209 The end of the growing season was assessed through a five stage leaf retention score based on a  
210 four stage scoring system originally developed by Worrell (2006) (a zero was added for no leaves).

211 As the trees were still relatively small, the assessment was made by estimating the percentage of the  
212 combined leaf area of the tree crown which was still green, not yellow or brown or had lost leaves.  
213 This was scored in the following categories

- 214  
215 0. No leaves present;  
216 1. One leaf present to 20% of crown green;  
217 2. 21-40% of crown green;  
218 3. 41-60% of crown green;  
219 4. 61-80% of crown green;  
220 5. 81-100% of crown green.

221  
222 For ash, sycamore and alder the growing season length was calculated by multiplying the bud  
223 development score or the leaf retention score by number of days. This gave a relative measure of  
224 photosynthetic duration. The growing season for cider gum, an evergreen tree could not directly be  
225 measured in the same way.

### 226 227 **Resource capture efficiency**

228  
229 For each of the twelve ash, alder and sycamore trees the influence of growing season and leaf area  
230 on growth was examined using a resource capture efficiency index, calculated by multiplying tree  
231 growing season (collected in 2011) by leaf area (collected in 2010). The formula and units of  
232 measurement are described below:

233  
234 Resource capture index = leaf area (m<sup>2</sup>) x growing season (leaf retention score x days)

235  
236 The relationship between stem dry weight in 2010 and resource capture efficiency was investigated.

### 237 238 **Statistical analysis**

239  
240 Statistical tests were conducted using IBM SPSS Statistics v19. The approaches used to test  
241 variables for significance of differences between species is described in Figure 1.

242  
243 <Figure 1 here>

244  
245 Regression was used to characterise relationships between L, W and LA and between L, W and  
246 LDW. IN SPSS there were eleven functions available for regression and the best-fit equation was  
247 selected by a combination of the smallest standard error of the estimate (SEE) and the highest R<sup>2</sup>.  
248 The same approach was used to define a relationship between stem dry weight and the resource  
249 capture efficiency.

### 250 251 **Results**

252  
253 Where non parametric approaches to analysis have been applied the median is shown as a measure  
254 of centrality, otherwise the mean for the data is presented.

### 255 256 **Stem volume and biomass**

257  
258 The stem volumes of the twelve trees of the four tree species for were assessed in late 2010 after  
259 two growing seasons and for the surviving three species in late 2011 after three growing seasons.  
260 The data for height, basal stem diameter and calculated volume are shown in Table 2. For the two  
261 and three growing seasons height, diameter and stem volume were compared between species and  
262 significant differences were found by species (Table 3).

263  
264 <Table 3 here>

265  
266 Table 3 shows the stem volume, specific gravity and stem dry weights after two growing seasons.  
267 Kruskal Wallis and Mann Whitney tests were applied to these data and significant differences were  
268 found and are described in Table 4. Medians for these data are shown.

269  
270 <Table 4 here>

271  
272 **Leaf Area**

273  
274 To determine leaf area, relationships between L, W and LA and between L, W and LDW were  
275 investigated. The results from best-fit regressions are described in Table 4 and Table 5. LA (Table 5)  
276 and LDW (Table 6) were estimated for the twelve trees of each species by applying the regression  
277 models to the L x W measurements for all but ash, where they were estimated from leaf stalk length.  
278 Kruskal Wallis test and Mann Whitney tests showed highly significant differences in leaf number, LA  
279 and LDW between species. The LA of alder and sycamore were not significantly different, but all  
280 others were significantly different. The LDW of cider gum was different from all others, but  
281 differences between the other species were not significant. In terms of leaf number, differences  
282 between ash and sycamore were not significantly but were significantly different from other species  
283 as were alder and cider gum.

284  
285 <Table 5 here>  
286 <Table 6 here>

287  
288 LAR and SLA was calculated for the four tree species and the median values are shown in Figure 2.  
289 Statistically significant differences in LAR and SLA were found between species.

290  
291 <Figure 2 here>

292  
293 Kruskal Wallis and Mann Whitney tests were applied to the LAR data and ash LAR was found to be  
294 significantly different from the other three species. Kruskal Wallis and Mann Whitney tests  
295 demonstrated that the SLA of all species were significantly different from each another, except for  
296 ash and cider gum. P values were significant for SLA and very highly significant for LAR.

297 **Growing season**

298  
299 The period of bud burst and senescence for ash, sycamore and alder for 2011 are shown in Figure 3.  
300 Alder had a longer growing season than the other two species, with an earlier and more rapid bud  
301 burst and a later and longer period leading up to complete leaf drop. Ash and sycamore showed a  
302 similar response, with sycamore having more rapid bud burst and being slower to drop its leaves.

303  
304 <Figure 3 here>

305  
306 Cumulative growing season index data was not normally distributed and a Kruskal Wallis test showed  
307 that differences in growing season between species were highly significant, while Mann Whitney  
308 tests showed that there were very highly significant differences between sycamore and alder, and  
309 ash and alder.

310  
311 **Characterising resource capture efficiency.**  
312

313 A correlation was performed of resource capture index against stem dry weight, which gave a R of  
314 0.729 and was very highly significant ( $p < 0.0001$ ). A regression was conducted and the best fitting  
315 function was quadratic (Figure 4,  $R^2 = 0.557$ ,  $SEE = 1.233$ ,  $y = -0.17x^2 + 0.683x + 2.267$ ).

316  
317 <Figure 4 here>

318  
319 As a comparison correlations were performed for the two components (growing season index and  
320 LA) separately of the resource capture index against stem dry weight. For growing season index the  
321 correlation with stem dry weight was relatively weak with a R of 0.444 and a high significance  
322 ( $p < 0.01$ ). In contrast the correlation between dry weight and LA was stronger with a R of 0.733 and  
323 was very highly significant ( $p < 0.0001$ ). A regression showed the best fitting function to be cubic  
324 (Figure 5,  $R^2 = 0.542$ ,  $SEE = 1.256$ ,  $y = -1.977x^3 + 2.132x^2 + 5.093x + 2.391$ ).

325  
326 <Figure 5 here>

## 327 **Discussion**

328  
329  
330 The winter of 2009-2010 was the coldest in the UK since 1978-1979 and the UK experienced the  
331 coldest December in 100 years (Prior & Kendon 2011). This was followed by another severe winter,  
332 which apart from that of 2009-2010, was the coldest since the winter of 1985-1986 (Anon 2011). The  
333 native and naturalised broadleaves were able to cope with these conditions, but the eucalypts fared  
334 badly, particularly the less cold-tolerant shining gum which exhibited complete mortality over each of  
335 the two severe winters. An analysis of the cold damage at the trial is described in Leslie, Mencuccini  
336 and Perks (2014). Eucalypts have been planted on a limited extent in the UK; between 2011 and  
337 2016 nurseries sold 220,000 transplants (Purse and Leslie 2016b) and this scale represented trial  
338 rather than commercial planting. However the limited information on suitable origins for cider gum  
339 (Cope, Leslie and Weatherall 2008) and shining gum (Evans 1986) suggests that the origins used in  
340 this trial were not particularly well adapted. Furthermore it is accepted that shining gum is one of the  
341 least hardy eucalypts planted in the UK and it is recommended that it be planted only within 20km of  
342 the coast in southern England and closer to the coast elsewhere in the UK (Purse and Leslie 2016a).  
343 The severely cold conditions and the origins planted explain some of the eucalypts poor  
344 performance.

345  
346 Of the tree species that survived the first winter, the largest stem volumes were achieved by cider  
347 gum and alder, with the eucalypt producing nearly twice the volume of alder (Table 3). Cider gum  
348 had accumulated the largest leaf area, which would partly explain the fast growth of this species  
349 (Table 5). The median leaf area of trees of alder ( $0.1919 \text{ m}^2$ ) was significantly different from ash  
350 ( $0.0627 \text{ m}^2$ ) and cider gum ( $0.4999 \text{ m}^2$ ), while that of sycamore ( $0.1856 \text{ m}^2$ ) was significantly different  
351 from cider gum. While ash had the lowest leaf area, it attained nearly the same stem volume as  
352 sycamore suggesting that it exhibits greater photosynthetic efficiency. Also, the leaf area of alder  
353 was not significantly different from sycamore yet it attained a significantly larger stem volume. These  
354 observations suggest sycamore has low photosynthetic efficiency. By the end of the third growing  
355 season cider gum had been killed in the winter of 2010-11 and the relative ranking of the remaining  
356 species in terms of stem volume remained the same.

357  
358 The leaf area of the trees was measured at the end of the growing season and this may not have  
359 fully captured the leaf area over the whole season, as it does not incorporate leaf turnover. There  
360 are considerable differences in leaf longevity between temperate tree species; mean leaf lifespan of  
361 alder is 90 days and in maples and oaks can be as long as 180 days. (Kikuzawa 1995). Leaf  
362 longevity may explain some of the differences found between species in SLA. The SLA of alder and  
363 sycamore was relatively high and cider gum and ash was relatively low (with no significant difference  
364 between the two). This suggests a greater allocation of resources per unit leaf area in cider gum and  
365 ash and less resources per unit leaf area in sycamore and alder. Generally there is a positive  
366 relationship between leaf mass: leaf area and the longevity of the leaves (Wright & Westoby 2002).  
367 Thus some trees invest relatively little in each metre of leaf area, allowing rapid build up of canopy,



368 fast cycling of leaves and high initial growth. In contrast other trees invest more heavily in each  
369 square metre of leaf area but retain these leaves for longer, resulting in a longer period of return from  
370 those leaves (Wright & Westoby 2002).

371  
372 In terms of SLA, this would suggest that trees which retain their leaves for longer periods will have a  
373 lower SLA and those with short leaf longevity have a high SLA. Alder leaves are retained by the tree  
374 for a relatively short period (Kikuzawa 1995) and so, as found in this study (Figure 2) exhibit a  
375 relatively high SLA of ( $8.8 \text{ m}^2 \text{ kg}^{-1}$ ) which would support such a strategy, each leaf being allocated a  
376 relatively low investment of resources. There are no studies of the leaf longevity of cider gum, but  
377 Whitehead and Beadle (2004) note that in general eucalypt leaves are thick, tough and long-lived, a  
378 reflection of their evergreen habit and their association with sites of low soil nutrients and mild  
379 winters. A study in Australia found *Eucalyptus paniculata* leaf lifespan to be 1.09 years and that of  
380 *Eucalyptus umbra* to be 2.06 years (Wright & Westoby 2002), but Laclau et al. (2009) studying  
381 *Eucalyptus grandis* in Brazil found unfertilised trees in plantation retained their leaves for 111 days.  
382 The relatively low SLA ( $4.9 \text{ m}^2 \text{ kg}^{-1}$ ) of cider gum (Figure 2) suggests a relatively long leaf lifespan.  
383 Ash also exhibited a low SLA and a study by Alberti et al. (2005) of older trees also found a low SLA  
384 for ash, compared with Wych elm (*Ulmus glabra*). Another characteristic of trees with high SLA, such  
385 as the alder and sycamore in this study, is that they tend to exhibit high photosynthetic nitrogen use  
386 efficiencies, whereas trees with a low SLA adopt a different strategy; absorbing a greater proportion  
387 of the light available through a higher chlorophyll content in the leaves (Poorter & Evans 1998).

388  
389 Statistically significant differences in specific gravity were found between species, with alder having a  
390 particularly low density (Table 4), also being lower than the  $0.540 \text{ Mg m}^{-3}$  cited by Claessens (2005 in  
391 Claessens et al. 2010), perhaps due to the young age of the trees. The specific gravity of ash was  
392 similar ( $0.550$  as opposed to  $0.560 \text{ Mg m}^{-3}$ ) to that found in larger trees from Italy (Alberti et al. 2005)  
393 and that of cider gum was similar ( $0.548$  as opposed to  $0.500 \text{ Mg m}^{-3}$ ) to that found in French  
394 plantations (AFOCEL 2003). The specific gravity was multiplied by stem volume enabling LAR (using  
395 stem weight rather than the conventional whole tree weight) to be calculated. This was compared by  
396 species and very highly significant differences were found between ash and all other species.  
397 Therefore ash supports a smaller leaf area per unit stem weight than sycamore, alder and cider gum  
398 (Figure 2). A shortcoming of this experiment was not to estimate branch and root weight of the trees,  
399 as this would have enabled a true LAR to be calculated and a better understanding of the relative  
400 allocation of resources between different parts of these trees. There are known to be differences in  
401 the allocation of resources between stem and leaves and roots between tree species (Poorter et al.  
402 2012). At the trial differences were observed; some individuals of shining gum exhibited instability  
403 due to excessive above ground growth and had fallen over, despite being supported by a tree shelter  
404 and bamboo cane. The other species showed good stability.

405  
406 Phenology of temperate trees is determined by temperature and photoperiod, with the importance of  
407 each of these factors varying with tree species (Basler & Körner 2012, Vitasse et al. 2012,). This  
408 study used visual assessment of budburst, which is the normal method used in field dormancy  
409 studies (Cooke et al. 2012). The pattern of bud burst and leaf fall between ash, alder and sycamore  
410 is illustrated in Figure 3. This shows that alder begins to come into leaf earlier than the other two  
411 species and also retains its foliage for longer into autumn and that ash flushes later and loses leaves  
412 earlier in autumn than the other two tree species. Basler and Körner (2012) found that there was no  
413 effect of photoperiod on bud burst of ash or sycamore, while a study (Vitasse et al. 2009) on the  
414 effect of temperature on budburst in seven temperate trees showed that of those planted at this trial,  
415 ash had the highest sensitivity to temperature, with sycamore being in the middle of the ranking.  
416 Spring 2011, when the assessment was made was particularly warm, being the warmest across the  
417 UK since 1910 (Met Office undated c). It is likely therefore that the growing season for 2011 was  
418 abnormally long for these species.

419  
420 The phenology data for ash, sycamore and alder were based on monitoring the development and  
421 senescence of leaves on the terminal bud but development of leaf area in trees is complex.  
422 Focusing on the terminal bud does not allow the pattern of whole tree leaf area to be examined and

423 pioneer trees tend to adopt a different approach to climax species. Climax or forest tree species  
424 show a flushing habit of leaf development, whereas pioneers show a successive pattern of leaf  
425 development (Kikuzawa 1995). The patterns of flushing between alder, ash and sycamore showed  
426 differences (Figure 3). The progression of leaf unfolding started earlier in alder but was also more  
427 gradual in alder than in the other two species, which exhibited rapid flushing over a relatively short  
428 period.

429  
430 Combining leaf area measurements from 2010 with growing season data from 2011 to create a  
431 resource capture index explained 56% of the differences in 2010 stem dry weight of the trees (Figure  
432 4). The best fitting relationship in terms of  $R^2$  was a curve but a linear relationship also provided a  
433 good fit ( $R^2=0.548$ ). The nature of the relationship is difficult to identify precisely because of the lack  
434 of data at the higher end of the combined leaf area and growing season index. A possible  
435 explanation for a curved relationship between growth potential index and stem dry weight is that light  
436 interception by canopies is not linearly related to leaf area index, but follows a similar curved  
437 relationship due to mutual shading of leaves (Cannell et al. 1989). This is supported by the curvilinear  
438 relationship between leaf area and stem dry weight (Figure 5). Using leaf area alone explained 54%  
439 of the variation in stem dry weight, only marginally poorer than combining leaf area and growing  
440 season. This can be explained by the relatively small differences in growing period between the tree  
441 species. Had the origins been collected across a wider range of latitudes it is likely that variation in  
442 growing season between species would have been greater.

443  
444 Growth is related to three variables; the site resources, the resource capture efficiency and the  
445 resource use efficiency (Stape et al. 2004). Multiplying leaf area by growing season provided a  
446 measure of the resource capture efficiency of the tree species at this trial. A combination of greater  
447 leaf area and longer period of growth has enabled alder to accumulate stem dry weight more rapidly  
448 than ash and sycamore (Figure 4). The rate of photosynthesis in a tree species is strongly linked to  
449 the nitrogen content of leaves due to large amount of leaf nitrogen devoted to chloroplasts (Poorter &  
450 Evans 1998) and alder, being a nitrogen fixing tree is likely to be able to devote larger concentrations  
451 of nitrogen to its leaves than the other species. This study also showed that alder exhibited a high  
452 SLA, (Figure 2) allocating relatively little biomass for every square metre of leaf area. Trees with high  
453 SLA are known to exhibit high photosynthetic nitrogen use efficiency (Poorter & Evans 1998) and in  
454 general high relative growth rates (Antinez et al. 2001). The higher leaf nitrogen concentration and  
455 this higher photosynthetic nitrogen efficiency may partly explain why alder has been able to build up  
456 leaf area rapidly and also use this leaf area efficiently. A further strength of alder is its relatively long  
457 growing season compared with sycamore and ash (Figure 3). Alder, is also known to have a short  
458 leaf longevity (Koike & Sanada 1989, Kikuzawa 1995), enabling it to replace damaged leaves rapidly.

459  
460 The most rapid growing species, cedar gum was able to develop the highest leaf area of any of the  
461 species over two growing seasons (Table 5), a contributory factor being that it retains leaves for more  
462 than one growing season. Other factors contributing to the high productivity are the long period of  
463 photosynthetic activity and the high photosynthetic efficiency known of eucalypts, particularly under  
464 conditions of high stomatal conductance (Whitehead & Beadle 2004). Furthermore, the opportunistic  
465 nature of eucalypt growth is likely to have enabled cedar gum to exhibit a longer growing season than  
466 alder.

467  
468 The leaf area of alder and sycamore were not significantly different (Table 5) and they both exhibit  
469 high SLA, yet alder had accumulated a greater stem dry weight (Table 4), due to a longer period in  
470 leaf and potentially due to higher leaf nitrogen content, allowing higher rates of photosynthesis (Koike  
471 & Sanada 1989). Ash was the slowest growing species, and had the lowest leaf area (Table 5) and  
472 the shortest growing period of the four tree species (Figure 3). Another factor may be low rate of  
473 photosynthesis in ash; a study by Koike and Sanada (1989) found that ash (*Fraxinus mandshurica*)  
474 had a relatively low rate of photosynthesis across soils with a range of levels of soil nitrogen, when  
475 compared with alder (*Alnus hirsuta*) and birch (*Betula maximowicziana*).

476

477 There were several limitations to this study. The method used to harvest leaves at the end of the  
478 growing season was unsuitable for ash and measuring leaf area at one point in time ignored potential  
479 turnover of leaves during the growing season. The approach used to measure growing season did  
480 not allow the estimation of growing season for cedar gum, an evergreen tree. This prevented a  
481 comprehensive comparison of the trees surviving the first winter. If the study was repeated the root  
482 and branch biomass would also be estimated to enable calculation of the LAR. Furthermore, growing  
483 season and leaf area was assessed in two different years and it would have been more consistent to  
484 measure these in the same year.

## 485 **Conclusion**

486  
487 It is clear that there are significant differences in growth between the tree species tested at this trial.  
488 By the end of the second growing season all shining gum, the fastest growing species had been  
489 killed by the cold winter of 2009-2010. Of the surviving three species, the species with greatest stem  
490 volume after two growing seasons was cedar gum followed by alder (Table 3). After three growing  
491 seasons none of the original eucalypts survived and alder exhibited the largest stem volume,  
492 although the specific gravity of the wood was less than the other species (Table 4). Cedar gum had  
493 developed a particularly high LA after two growing seasons, with alder and sycamore following with  
494 LA that were not significantly different (Table 5). However, alder had grown much more quickly and  
495 its longer growing season (Figure 3) may contribute to this higher growth rate. LAR (stem weight)  
496 was particularly low for ash (Figure 2), indicating that ash allocates less relative resources to leaves  
497 than to its stem. SLA was also low for ash, as well as cedar gum indicating that these species invest  
498 relatively high resources in each unit area of leaf area, relative to alder and sycamore (Figure 2).  
499 The strong influence of LA and growing season on productivity was shown by creating a resource  
500 capture efficiency by multiplying growing season by LA, and this explained 56% of the variation in  
501 stem dry weight between trees (Figure 4), however this was only marginally better than LA alone  
502 (Figure 5). It is likely that growing season would have a greater influence on growth if origins had  
503 been selected from a wider range of latitudes.

504  
505 The results show that for biomass production on similar sites, alder would be a good candidate, being  
506 capable of rapidly accumulating LA and exhibiting a long growing season, resulting in high  
507 productivity. However, studies have shown that stands of alder emit N<sub>2</sub>O, which may possibly make it  
508 less attractive as a candidate tree for sequestration of greenhouse gas (Arnold et al. 2005, Mander et  
509 al. 2008).

## 510 **List of abbreviations**

511  
512 L: length of leaf  
513 LA: leaf area  
514 LAR: leaf area ratio  
515 LMF: leaf mass fraction  
516 LDW: leaf dry weight  
517 M: oven dry weight of stem  
518 RGR: relative growth rate  
519 S: length of petiole and main midrib in ash  
520 SG: specific gravity  
521 SLA: specific leaf area  
522 V: stem volume  
523 W: maximum width of leaf

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540

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697  
698

699 Table 1 Origins of trees used in the trial and recommendations for the origins. A map of regions of  
 700 provenance (Zones) for Great Britain is available in Forestry Commission (undated).

Species	Origin	Recommendations
Alder	Zone 108, South west Scotland	Use British provenances <sup>1</sup> .
Ash	Zone 108, South west Scotland	Seed stand material or material slightly to the south of planting site <sup>2</sup> .
Birch	Zone 202, central to north east Scotland.	Avoid origins from long distances away from the planting site (slightly southern/ eastern locations seems to give more rapid growth) <sup>2</sup> .
Cider gum	Likely to be from a seed stand at Dipton, New Zealand <sup>3</sup> . Original origin unknown.	Origins from Lake McKenzie and Mount Cattley, Tasmania perform particularly well <sup>4,5</sup> .
Shining gum	Likely to be from a seed stand at Dipton, New Zealand <sup>3</sup> . Origin Central Victoria	Victoria provenances are most frost hardy <sup>4</sup>
Sycamore	Zone 403, Midlands, England	Most British provenances grow well at most sites. May increase productivity by using origins from sites slightly to the south of the planting site <sup>2</sup> .

701 Recommendations from <sup>1</sup>Worrell (1992) <sup>2</sup>Hubert and Cundall (2006), <sup>3</sup>Purse pers. comm. 2009a,  
 702 <sup>4</sup>Evans (1986), <sup>5</sup>Cope, Leslie and Weatherall (2008)

703  
704

705 Table 2 Climate at the trial from the Establishment Management Information System<sup>1</sup> and from 1971  
 706 to 2000 average data from the Newton Rigg weather station<sup>2</sup> (Met Office undated a, except for  
 707 minimum temperature, which is from Met Office undated b)

AT5 <sup>1</sup> (degrees yr <sup>-1</sup> )	CT <sup>1</sup> (°C)	DAMS <sup>1</sup>	MD <sup>1</sup> (mm)	Summer Rainfall (mm) <sup>1</sup>	Winter Rainfall (mm) <sup>1</sup>	Mean Min Temp (°C) <sup>2</sup>	Min Temp (°C) <sup>2</sup>	Frost days <sup>2</sup>	Mean Max Temp (°C) <sup>2</sup>
1503.4	6.3	14	148.2	386.4	396.2	0.4 (Jan)	-14°C	57.6	19.4 (Jul)

708 AT5 = Accumulated temperature above 5°C, CT=continentality, DAMS = Detailed aspect method of scoring, MD = moisture  
 709 deficit. A detailed description of these variables is found in Pyatt et al (2001). Annual rainfall = summer rainfall + winter  
 710 rainfall.

711  
712



713 Table 3 Height, stem diameter and volume for each species after two and three growing seasons.

Species	2 growing seasons			3 growing seasons		
	Height <sup>1</sup> (cm)	Diameter <sup>2</sup> (mm)	Stem volume <sup>2</sup> (cm <sup>3</sup> )	Height <sup>3</sup> (cm)	Diameter <sup>3</sup> (mm)	Stem volume <sup>2</sup> (cm <sup>3</sup> )
Alder	155.5a	28.7a	9.6a	194.5a	43.8a	23.0a
Ash	119.0b	20.7b	6.4b	133.8b	27.4b	9.5b
Cider gum	199.5c	35.7c	18.0c	-	-	-
Sycamore	134.0ab	14.3b	4.9b	162.0ab	20.0b	8.1b

714 <sup>1</sup>Anova and Tukey's test (Mean shown), <sup>2</sup>Kruskal Wallis and Mann Whitney U test (Median shown),

715 <sup>3</sup>natural logarithm transformed then Anova and Tukey's test (Mean shown). The same lower case

716 letter (a, b or c) denotes no significant difference between species.

717

718

719 Table 4 Specific gravity (SG) and calculated stem dry weight (M) after two growing seasons from 12  
720 randomly selected trees of each species.

<b>Species</b>	<b>Specific gravity (g cm<sup>-3</sup> = Mg m<sup>-3</sup>)</b>	<b>Stem dry weight (g)</b>
Alder	0.391a	3.759a
Ash	0.563b	3.539ab
Cider gum	0.553c	9.896c
Sycamore	0.497c	2.390b

721 Kruskal Wallis and Mann Whitney U test applied to specific gravity and stem dry weight (Medians  
722 shown). The same lower case letter (a, b or c) denotes no significant difference between species.

723 Table 5 Description of the models predicting leaf area where y is mean area of one leaf (LA) in cm<sup>2</sup>  
 724 and x is L (cm) x W (cm) of the leaf, except for ash where x is leaf stalk length and median leaf area  
 725 by species. Total tree LA was calculated by multiplying number of leaves by the mean area of one  
 726 leaf and converted in m<sup>2</sup>.

Species	Number leaves	Regression model	R <sup>2</sup>	SEE	Median tree LA (m <sup>2</sup> )
Alder	202a	$y=0.325x^{1.102}$	0.941	0.202	0.1919a
Ash	22b	$y = 0.1201x^{2.1891}$	0.707	0.524	0.0627b
Sycamore	25b	$y= 0.532x^{1.021}$	0.964	0.197	0.1856a
E. gunnii (mature)	657c	$y=0.052x^2+0.448x+1.032$	0.967	0.947	0.4999c
E. gunnii (juvenile)		$y=0.7714x^{0.943}$	0.881	0.216	

727 Table 6 Description of the models predicting leaf area where y is LDW of a leaf in grammes and x is  
 728 L (cm) x W (cm) of the leaf, except for ash where x is leaf stalk length. Whole tree LDW was  
 729 calculated by multiplying number of leaves by the mean dry weight of a leaf.  
 730

Species	Regression model	R <sup>2</sup>	SEE	Median tree LDW (g)
Alder	$y=0.054+0.001x+0.0000751x^2-0.000000292x^3$	0.967	0.041	21.75a
Ash	$y = 0.004x^2 + 0.005x - 0.029$	0.853	0.187	12.44a
Sycamore	$y=0.007-0.20x$	0.970	0.099	23.63a
E. gunnii (mature)	$y=0.010x+0.001x^2+0.029$	0.981	0.017	100.98b
E. gunnii (juvenile)	$y=0.012x+0.021$	0.932	0.300	

731  
 732

733 Figure 1 Approach used to determine significance of differences between variables.  
734  
735 Figure 2 Leaf Area Ratios (LAR) and Specific Leaf Areas (SLA) for the four tree species (Different  
736 letters above the bars indicates a significant difference, confidence intervals are not given because of  
737 lack of normality).  
738  
739 Figure 3 Bud burst and leaf retention of ash, sycamore and alder over the growing season of 2011.  
740  
741 Figure 4 Stem dry weight against resource capture efficiency.  
742  
743 Figure 5 Stem dry weight against leaf area.  
744  
745  
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747